BREEDING BIOLOGY OF TRISTRAM'S STORM-PETREL (OCEANODROMA TRISTRAMI) IN A CHANGING ENVIRONMENT

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by

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ABSTRACT

The effects of invasive ants on the nesting success of Tristram's Storm-petrel (*Oceanodroma tristrami*) were documented over the course of two breeding seasons on Laysan and Tern Islands, Northwestern Hawaiian Islands. On Laysan Island, *Monomorium pharaonis* was responsible for 1% of nest failures and did not significantly affect Tristram's Storm-petrel breeding success. On Tern Island, *Pheidole megacephala* was not found to affect nesting Tristram's Storm-petrels. Despite these findings, more research is required to examine the effects of weather and seasonality on these relationships. Tristram's Storm-petrel had a relatively low reproductive rate on Laysan (0.16), Tern (0.28), and East (<0.22) islands. Nest abandonment was the greatest cause of nest failure followed by nest site competition with larger burrowing seabirds and weather effects. Future research should focus on Tristram's Storm-petrel demography, age of first breeding, and breeding success on islands with different topography such as Nihoa. Six and five species of ant were recorded on Laysan and Tern Islands, respectively.

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CHAPTER 1

INTRODUCTION AND OVERVIEW

1.1 BACKGROUND INFORMATION

1.1.1 Biological Invasions and Invasive Species

The natural ecosystems that evolved in isolation on islands and those on large landmasses have increasingly become interconnected due to human assisted dispersal by deliberate or inadvertent transport of biological material across dispersal barriers (Mooney 2005). This has resulted in tens of thousands of terrestrial, marine, and freshwater organisms ranging from microbes, algae, plants, invertebrates and vertebrates being moved around the world every day through a wide variety of human-driven pathways (Carlton and Ruiz 2005). Though few of these alien species will become established and even fewer will have highly deleterious effects on native communities (Byers et al. 2002), collectively they have invaded virtually every ecosystem on our planet and a few are responsible for the extinctions of hundreds of native species (De Poorter et al. 2005). These invasions have also altered evolutionary trajectories, disrupted community and ecosystem processes, caused large economic loss, and threatened human health (Mooney 2005). Invasions are problematic on local, regional, and continental scales (Hobbs and Mooney 2005) and thus are instruments of change on a global scale (Vitousek 1996).

An invasive species is one that becomes newly established in natural or semi-natural ecosystems or habitat, is an agent of change, and threatens native biological diversity (IUCN 2000). Invasive species occur in all taxonomic groups (De Poorter et al.

2005) and there is no universal theory of invasion due to the numerous mechanisms involved (Stachowicz and Tilman 2005). However, invaders generally have rapid growth to maturity, are able to adapt to environmental stress, and have a high tolerance to environmental heterogeneity (Baker 1965). Exotic species prosper in their new range in part because many of their natural predators and parasites are absent, a theory known as the "enemy release hypothesis" (Keane and Crowley 2002, but see Liu and Stiling 2006). Disturbance, competitive hierarchies, and a number of other factors may also play a role in to what degree an invasive may prosper (Bruno et al 2005). Facilitative interactions, where one invader increases the likelihood of survival and ecological impact of another, are increasingly frequent and substantial issues (Simberloff 2006).

1.1.2 Island Ecosystems and Invasive Species

Even in remote locations, where human activities are inconsequential by global standards, high rates of biological invasion are a pervasive feature of the landscape (Gaston et al. 2003). Islands are not necessarily inherently easier to invade (D'Antonio and Dudley 1995). However, they do appear to be especially susceptible to the impacts of invasive species due to their long isolation from some of the selective forces that have shaped the evolution of continental organisms' self-defence mechanisms and competitive ability (Loope et al. 1988). It does appears that the greater the isolation of the island, the greater the severity of the impact, likely because of the relaxation of selective forces in species-depauperate remote island ecosystems (Whittaker 1998). As a result, the human-driven introduction of invasive alien species can be considered the most important cause of island biodiversity loss and the greatest threat to island ecosystems (Clout and Veitch

2002). Invasive alien species can cause widespread diversity loss through direct predation, degradation of habitat through herbivory, competition, and transmission of disease (Park 2004). These effects may be simple or complex, as many invasive alien species can be present simultaneously and interact among themselves as well as with indigenous species (Courchamp et al. 2003).

1.1.3 Seabirds and Invasive Species

Most seabirds nest on islands that do not harbour predators (McChesney and Tershy 1998) resulting in an absence of selection pressure that would usually lead to the evolution of anti-predator behaviour such as hiding their sounds, scents, or their nests from predators (Courchamp et al. 2003). In addition, in response to scarcity of resources in the marine environment (Rahn and Whittow 1984) seabirds have evolved a life history strategy that favours adult survival at the cost of low fecundity and late age of first breeding (Courchamp et al 2003). This leaves seabirds extremely vulnerable if predators are introduced as they are without both behavioural and reproductive defences (Loope and Mueller-Dombois 1989). Invasive predators have caused severe declines, extirpation, and extinctions (reviewed in Burger and Gochfeld 1994, Moors and Atkinson 1984, Jones and Byrd 1979) and are a leading threat to seabird populations world-wide (Keitt and Tershy 2003).

Among seabirds, storm-petrels (Family Hydrobatidae) are among the most vulnerable to predation (King 1973). Storm-petrels have evolved to be primarily nocturnal on land and nest in burrows to avoid avian predators (Watanuki 1986), but these adaptations are of little use against terrestrial predators. The smallest of seabirds,

storm-petrels are delicate in build, poor walkers on land and vulnerable in the open (Brooke 2004). They have little chance defending themselves against even the smallest of introduced terrestrial predators and are often extirpated following introductions (De Leon et al. 2006). The presence of introduced predators is now the limiting factor of most storm-petrel species (De Leon et al. 2006, Slotterback 2002, Ainley and Everett 2001) and has led to the loss of the Guadalupe Storm-petrel (*Oceanodroma macrodactyla*), presumably extinct due to predation by introduced cats (Jehl and Everett 1985).

1.1.4 Invasive Arthropods on Islands

The effect of invasive vertebrates on islands has received a great deal of attention (Kerbiriou et al. 2004, Huyser et al. 2000, Bailey 1993, etc.). Invasive arthropods are poorly studied in comparison, despite the fact that they comprise the overwhelming majority of invasive animal species on remote islands. For example, of the over 5 000 documented alien species in Hawaii, over 3 500 are arthropods (Eldredge and Evenhuis 2003) with between 15 and 20 new introductions each year (Beardsley 1979). Invasive arthropods can be difficult to research because their effects are often more subtle and harder to separate from effects of other perturbations such as habitat loss and fragmentation and environmental stochasticity (Hansen et al. 2002). To further complicate matters, there is often substantial lag time between introduction and discovery of invasive arthropods. Often only after their impact has become severe and often irreversible are many invasive arthropods recognized (Loope and Howarth 2002).

In terms of their effects on endemic vertebrates, the most studied group of invasive arthropods on islands are ectoparasites (mosquitoes, mites, and flies). Parasitic species that evolved host population-parasite relationships rarely cause serious harm to their native host populations. However, when brought into contact with a parasite-free population, the new host may suffer significant mortality before defence mechanisms can evolve (Fessel and Tebbich 2002). Ectoparasites have the greatest ability to negatively affect endemic fauna as vectors for disease. New pathogenic microorganisms likely have arrived onto even very remote islands (van Riper III 1991). However, these pathogens typically may not spread to endemic fauna unless a vector, such as a biting insect, is present. When a vector is introduced, the effect can be devastating to island fauna which often evolved in a pathogen-scarce environment (Wikelski et al. 2004). This is further complicated by the fact that island endemics are often slow to evolve resistant genotypes due to their often small population sizes and low levels of genetic heterozygosity (Simberloff 1995). The devastating effects of invasive arthropods as disease vectors is perhaps best demonstrated with the introduction of *Culex quinquefasciatus*, a nocturnal tropical mosquito, to the Hawaiian Islands. *Culex quinquefasciatus* is capable of transmitting the protozoa *Plasmodium relictum capistrnoae*, the species responsible for avian malaria in Hawaii (van Riper III 1991). Malaria was likely the primary cause of the second phase of extinctions of Hawaii's endemic avifauna in the early 1900's and is currently the limiting factor in the recovery of several species of forest bird (van Riper III and Scott 2001).

Invasive arthropods can affect island ecosystems in a variety of other ways. Invasives often feed on endemic plant species and can cause severe defoliation and

damage (Dowd et al. 2003). They can also compete directly with native arthropods for host plants and have the potential to disrupt the pollination of native plants by changing the pattern of pollination among plants and through stealing nectar (Howarth 1985). While disrupting the pollination of native plants, invasive arthropods may also become the main pollinators of invasive plants, further altering the ecosystem (Howarth 1985).

Invasive arthropods, including social insects, can also have profound effects by preying on native species of arthropods. In addition to the threat of extinction and biodiversity loss, this can disrupt ecosystems in a number of ways. Many island plants have evolved with a single specialized pollinating (arthropod) species. The elimination of the pollinator is likely to mean the elimination of the plant (Loope et al. 1988). Interference with nutrient cycling, and resource competition with both native predatory invertebrates and vertebrates are also possible effects (Howarth 1985). These impacts are often amplified and diversified by the presence of multiple invasive arthropods. An example is the rapid and severe ecosystem shift on Christmas Island where Dowd et al. (2003) found that invasive crazy ants (*Anoplolepis gracilipes*) extirpated red land crabs (*Gecarcoidea natalis*) from invaded areas. Red land crabs were a keystone species and the dominant consumer on the forest floor. Their absence changed the composition of the forest and slowed litter breakdown. At the same time, ants increased the number of invasive scale insects. Dense populations of scale insects lead to canopy dieback and the death of canopy trees. Therefore, the introduction of a single species of ant on Christmas Island was responsible for drastic ecosystem alteration on at least three trophic levels.

1.1.5 Invasive Ants

Ants are one of the most successful fauna on earth due to their intricate social structures that allow them to function in a cooperative and coordinated manner (Holldobler and Wilson 1990). Of the thousands of classified ant species, approximately 150 have become widely dispersed by humans and have been termed "tramp ants" (McGlynn 1999). Invasive ants form a distinct group within the tramp ants, the qualification being that while tramp ants are most often associated with human structures and urban environments, invasive ants penetrate natural ecosystems following introduction (Holway et al. 2002).

Invasive ants appear to share a number of characteristics that allow them to penetrate and dominate native ecosystems (Tsutsui and Suarez 2003). Many invasive ants appear to exaggerate the cooperative behaviour observed in all social insects. When introduced to a new environment, invasive ants often alter their colony structure from small territorial communities into territorially vast and numerically dense supercolonies (Tsutsui and Suarez 2003), a behaviour termed unicoloniality. Unicoloniality is often associated, but should not be confused with, polygyny, the practice of having multiple queens in colonies. Though unicolonial nests are often polygynous, a polygynous nest may not necessarily work in cooperation with other neighbouring nests. Unicoloniality provides a distinct advantage to invading ants, as the species is without the costs associated with intraspecific aggression and territoriality, permitting more resources towards colony growth, resource defence, and interspecific competition (Holway et al. 1998). These advantages ultimately allow the invasive ant to attain an extremely high local abundance and dominate the habitat (Holway et al. 2002).

Another characteristic stemming from the intricate social structure of ants is competitiveness and effective predator defence. Even in their native habitats, ants are efficient exploiters of food resources (Holldobler 1976). Numerous and specialized members of the colony allow ants to search large areas for resources, efficiently share food resources, and guard concentrated sources that cannot be transported back to the colony (Moller 1996). This advantage becomes formidable when considering that most ant species evolved in competition with other ant species and formed hierarchies based on aggressiveness (Vepsalainen and Savolainen 1990). The aggressive species at the top of these hierarchies are often the most successful invaders, quickly recruiting to and defending resources (Lubin 1984). Nest defence may also play a role. Colonies are often vigorously defended, leading to few effective nest predators (Wheeler 1910). In some invaded habitats, specifically remote oceanic islands, endemic predators of native arthropods may be missing entirely (Simberloff 1995). In addition, because the colony as a whole is the key reproductive unit in ants, losses of individuals are relatively inconsequential and nest-centred predation is the only threat once a colony becomes established (Moller 1996).

An additional attribute generally shared by invasive ants is generalized nesting and foraging. Nesting behaviour is especially important at the dispersal stage, as greater flexibility in nesting substrate allows for a wider range of introduction vectors through products of human traffic and commerce. The behaviour of relocating nests following disturbance or to exploit favourable sites may also increase a colony's chance of being dispersed by humans (Holway et al. 2002). Once dispersed, this same flexibility increases the number of habitats that may be invaded. Flexibility of diet may also be key

to invasion success. Though it is often difficult to assess the diets of invasive ants, they are opportunistic feeders, exploiting both protein (scavenging carrion, actively preying upon invertebrates and vertebrates), and carbohydrate (plants and insect exudates) resources (Holway et al. 2002).

1.1.6 Invasive Ants and Birds

There is considerable correlative and limited experimental evidence that invasive ants are capable of causing declines in vertebrate populations including small mammals, reptiles, and birds (Holway et al 2002). How invasive ants affect birds is often unclear and understudied (Holway et al. 2002), but it can include both direct and indirect effects. Direct effects include predation, most often involving the chick (Hooper-Bui et al. 2004, Mueller et al. 1999, Sikes and Arnold 1986). Mortality of chicks may also occur from harassment by invasive ants, which increases the energy expenditure of chicks while reducing time available for sleeping and foraging (Gerlach 2004, Giuliano et al. 1996, Pedersen et al. 1996). Indirect effects are less studied and difficult to quantify. Invasive ants may reduce the suitability of nest sites (Ridlehuber 1982), altering the distribution patterns of breeding birds and potentially forcing them into more marginal habitats (Suarez et. al 2000). There is also the potential for declines in bird populations due to resource competition with invasive ants, specifically insectivorous birds (Wetterer et al 1998, Allen et al. 1995, Banko and Banko 1976). Though potentially biased by the predominance of studies focussing on the red imported fire ant (*Solenopsis invicta*), ground-nesting birds with altricial young appear to be more vulnerable to the negative effects of invasive ants.

1.1.7 Rationale

Invasive ants are present on all Northwestern Hawaiian Islands with significant bird populations (Nishida 2001). The avifauna of the Northwestern Hawaiian Islands would appear to be exceptionally susceptible to the negative effects of invasive ants. Comprising 22 native species, the avifauna of the archipelago are either ground-nesting or make use of vegetation of less than 2 m in height with chicks confined to the nest for up to several months. Finally, the birds of the archipelago lack defensive behaviour that could potentially mitigate negative effects of invasive ants because they have evolved in the absence of social insects.

Of greatest concern is Laysan Island. The island is the most important in the archipelago in terms of avifauna, housing the greatest number of seabirds overall and the second highest number of species of all island groups in the archipelago (Fefer et al. 1984). Of equal importance is the presence of two endemic land bird species, the Laysan Duck (*Anas laysanensis*) and the Laysan Finch (*Telespiza cantans*). Laysan also has the highest diversity of invasive ants recorded in the refuge with nine (Nishida 2001). Past observations have suggested invasive ants are negatively affecting the breeding success of birds, including island endemics (Conant and Rowland unpublished). These include reports from Laysan Island of *Monomorium pharaonis* (L.) on dead Laysan Finch (*Telespiza cantans*) chicks that had been healthy the previous day, and *Tetramorium bicarinatum* (Nylander) harassing Red-tailed tropicbird (*Phaethon rubricauda*) chicks. However, both Laysan Finches and Red-tailed Tropicbirds nest at relatively low densities on Laysan (Morin and Conant 2002, USFWS unpublished). To study these species

would require extensive sampling effort over a large study area to achieve the needed sample size from which to draw strong conclusions. Instead, this study focuses on Tristram's Storm-petrel (*Oceanodroma tristrami*). This species is the smallest of Laysan's breeding seabirds at an average of 92 g (Marks and Leasure 1992). In addition, Tristram's Storm-petrel has one of the longest breeding seasons in the archipelago, with an average incubation length of 44 days and an average fledge length of 83 days (Chapter 2), thus both adult and chick live for long periods in habitats that possibly expose them to ant harassment. Tristram's Storm-petrels are also colony nesters meaning they can be found in relatively high densities that would be more amenable to small scale experimental manipulation.

Another island of concern is Tern Island, French Frigate Shoals. The invasive ant present on Tern island, *P. megacephala,* is present on several Northwestern Hawaiian Islands (Nishida 2001), demonstrates extremely aggressive behaviour, and is capable of achieving extremely high densities (Gillespie and Reimer 1993). Recent observations on Tern Island, French Frigate Shoals suggest that *P. megacephala* is a contributing factor in the death of Tristram's Storm-petrel chicks (McClelland and Jones personal observation) and anecdotal evidence suggests *P. megacephala* may be having a negative effect on birds on other islands in the Northwestern Hawaiian Islands (Krushelnycky et al. 2005).

*1.1.8 Tristram's Storm-petrel (*Oceanodroma tristrami*)*

Tristrams's Storm-petrel is both the most massive of the storm-petrels and the only member of their avian family that breeds in the Northwestern Hawaiian Islands (Figure 1.1). It is also one of the few members of its genus to breed in the boreal winter.

Because of the remote nature of its breeding sites and the timing of its breeding season, few studies have been conducted on the species and basic knowledge of life history, at sea distribution, and population status is very poorly known (Marks and Leasure 1992). Breeding biology has been studied at a single colony, Laysan Island (Marks and Leasure 1992). This study was hampered by high nest abandonment rates that consequently led to small sample sizes, thereby, restricting the strength of conclusions that can be reached. With the exception of Pearl and Hermes Reef (Wegmann and Kropidlowski 2002) all population estimates of Tristram's Storm-petrel for Hawaii are based on brief visits to islands and are over 20 years old (see Rauzon et al. 1985). As a result, Tristram's Storm-petrel is considered a species of conservation concern by the U.S. Fish and Wildlife Service (2002a). A summary of all research and observations of Tristram's Storm-petrel in the Northwestern Hawaiian Islands is presented in Appendix I.

1.1.9 Pharaoh Ant (Monomorium pharaonis) (Linnaeus)

Due to human activity, *M. pharaonis* has been carried to "all the inhabited regions of the globe" (Wheeler 1910) and is possibly the most widespread ant species in the world (Edwards 1986, Delabie and Blard 2002). In fact, *M. pharaonis* has become so widespread that its original place of origin may never be known (Vail and Williams 1994). Colonies of *M. pharaonis* are polygynous and unicolonial, and spread through the process of sociotomy or "budding", where new nests are established by groups of workers carrying brood stages to a new nest site (Edwards 1986). These new nests are often highly mobile and perhaps the most critical to *M. pharaonis*'s success in being spread by humans (Buczkowski et al. 2005). The species is omnivorous and has been

described as an aggressive scavenger (Deyrup et al. 2000), but it is most often associated with human structures and urban environments (Edwards 1986). As a result, it is more often referred to as a tramp ant as opposed to an invasive.

*1.1.10 Bigheaded Ant (*Pheidole megacephala*)* (Fabricus)

Originally of African origin (Cornelius and Grace 1997), *P. megacephala* is a widely dispersed tropical invasive, introduced to Hawaii in the late 1870's (Perkins 1913). Despite its status as a major pest in many areas, little is known about the biology of *P. megacephala* (Loke and Lee 2004). However, it is known that the species is unicolonial, polygynous, omnivorous, and has generalized nesting requirements (Hoffman 1998). *Pheidole megacephala* is an extremely efficient and aggressive predator of invertebrates (Illingworth 1917) and is a threat to biodiversity wherever it is introduced (Hoffman 1998). This is perhaps best demonstrated in Hawaii where is has been implicated as the major cause of the loss of all the native arthropods in lowland ecosystems (Perkins 1913, Zimmerman 1970). *Pheidole megacephala* is also a serious crop pest due to its propensity towards mutualistic interactions with homopterous pests that spread plant diseases in tropical food crops (Reimer et al. 1990).

1.2 STUDY LOCATIONS

1.2.1 Laysan Island

Laysan Island (25°46 N, 171°03' W) is the largest island in the Hawaiian Islands National Wildlife Refuge. Located 1495 km northwest of Honolulu, Laysan is a 397 ha

coral sand island featuring a 70 ha hypersaline lake in the centre (Figure 1.2). Guano mining commenced on Laysan in 1891 and did not cease until the early 1900s. During that time rabbits were introduced to the island and initial attempts to eradicate them following the abandonment of mining operations failed (Ely and Clapp 1973). By 1923, the rabbits had stripped Laysan almost completely of all vegetation, (Christophersen and Caum 1931), leading to the extinction of three endemic land birds and the extinction or extirpation of at least ten plant and an untold numbers of arthropod species (Morin and Conant 1998, Asquith 1994). Laysan is currently in the midst of an island restoration project undertaken by the U.S. Fish and Wildlife Service. In 2004 approximately 217 ha, or 66% of available area, was vegetated (McClelland unpublished). However, it remains a very different ecosystem from what it was before human occupation (Morin and Conant 1998). Laysan has not been extensively surveyed for ants since 1990 (Conant and Rowland unpublished), leaving the current ant community relatively unknown.

1.2.2 French Frigate Shoals

French Frigate Shoals is located almost exactly at the midpoint of the 2500 km-long Hawaiian archipelago, lying between the latitudes of 23° 37' 18" and 23° 52' 50" North and the longitudes 166° 03' 14" and 160°20' 04" West (Amerson 1971). It is a crescent-shaped atoll framed by an almost continuous outer reef 57 km in length and an inner reef measuring 33 km (Figure 1.3). The atoll can at any time contain between 12 and 16 sand islets that range greatly in permanence and stability. Currently, Tern and East Islands are the only islands known to have Tristram's Storm-petrel colonies in the shoals, but La Perouse Pinnacle may also support a breeding population (Chapter 2).

1.2.3 Tern Island

Located at the northwest tip of the crescent, Tern Island is the largest island in the shoals (Amerson 1971). Originally Tern Island was a naturally-occurring 4.5 ha island measuring 1 km by 135 m, rising up to 3.5 m above sea level, with low vegetation and bird colonies located on the western half (Amerson 1971). In 1942 the U.S. Navy converted Tern Island into a Naval Air Station. The island was enclosed with a steel sheet pile bulkhead and filled with crushed coral from the surrounding reef expanding the island's dimensions to 14 ha (USFWS 2002b). The U.S. Navy abandoned the island at the end of World War II after which it remained unoccupied until 1952 when the U.S. Coast Guard converted it into a Long Range Aid to Navigation (LORAN) station (USFWS 2002b). U.S. Fish and Wildlife came into possession of the island in 1979, converting it into a permanently staffed research and monitoring station.

Today Tern Island is still surrounded by the bulkhead, now in poor condition with some portions having corroded and failed. A rock revetment wall was installed around the western half of the island in 2004 to protect several buildings required to maintain the research station. Tern Island retains its airstrip, leaving 16 acres of available habitat which 16 species of seabird use for breeding (USFWS 2002b). The island is vegetated by 18 plant species (USFWS 2002b). The island has been surveyed for invasive ants several times since 1990 (Richardson 2000) with the current ant fauna presented in Appendix II.

1.2.4 East Island

East Island is located 6 miles southeast of Tern Island. Irregularly shaped, it measures 650 m feet at its longest point and 80 m at its widest but totals only 4.5 ha (Amerson 1971). Only the northern half of the island is vegetated (McClelland personal observation). Hawaiian Green Sea Turtles (*Chelonia mydas*) nest in large numbers on East and severely disturb the island's surface with their nest pits every summer. Aside from a single 30 m wooden pole and some cement rubble, little marks the island's past as a USCG station from 1944 to 1952.

1.2.5 La Perouse Pinnacle

La Perouse Pinnacle is a basaltic plug located 9.5 km south-southeast of Tern Island. Rising 37 m at its highest, it is all that remains of the original volcanic island around which the coral reef established itself, forming the shoals. The main rock is approximately 225 m long and 50 m wide. The base is black while the upper portion appears white due to guano deposits that can be found at depths of up to1 m (Amerson 1971).

1.3 PURPOSE AND GOALS OF STUDY

1.3.1 Study Questions

The objectives of this study were to identify and quantify the impacts of invasive ants on the nesting success of Tristram's Storm-petrel in the Northwestern Hawaiian Islands and to determine whether or not a control or eradication program should be implemented

by USFWS. Basic knowledge vital to the conservation of Tristram's Storm-petrel remains poorly understood, therefore, a secondary goal of this study was to elucidate the basic breeding biology and population levels of Tristram's Storm-petrel on study islands. To accomplish these goals, three questions were asked, and the findings reported here:

1. What is the basic breeding biology and population size of Tristram's Storm-petrel on Laysan Island and French Frigate Shoals?

2. What are the current alien ant communities of Laysan Island and French Frigate Shoals?

3. Do the alien ants that are currently present significantly impair the breeding success of Tristram's Storm-petrel in the Northwestern Hawaiian Islands?

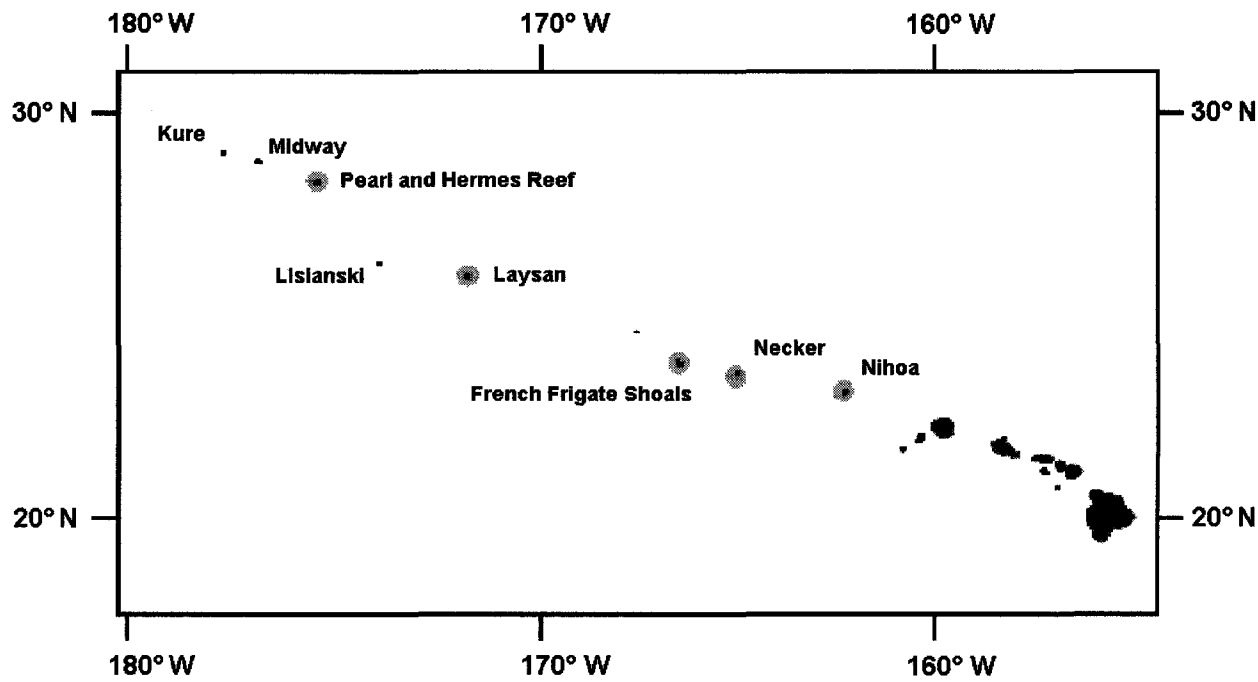

Figure 1.1: The Hawaiian Islands archipelago. The current breeding distribution of Tristram's Storm-petrel is represented by light grey.

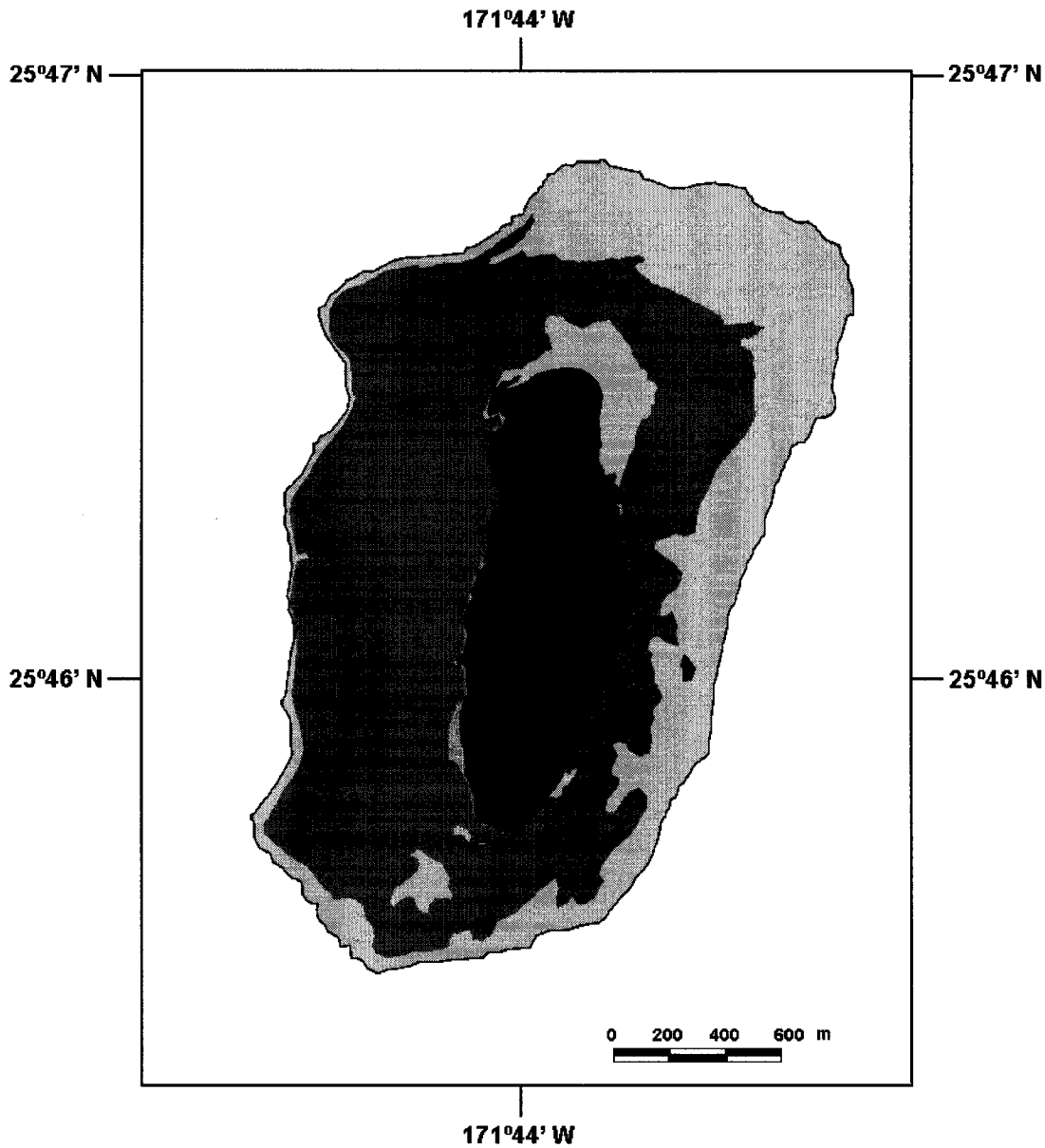

Figure 1.2: Laysan Island, Northwestern Hawaiian Islands. Vegetation is represented by dark grey, the hypersaline lake by black.

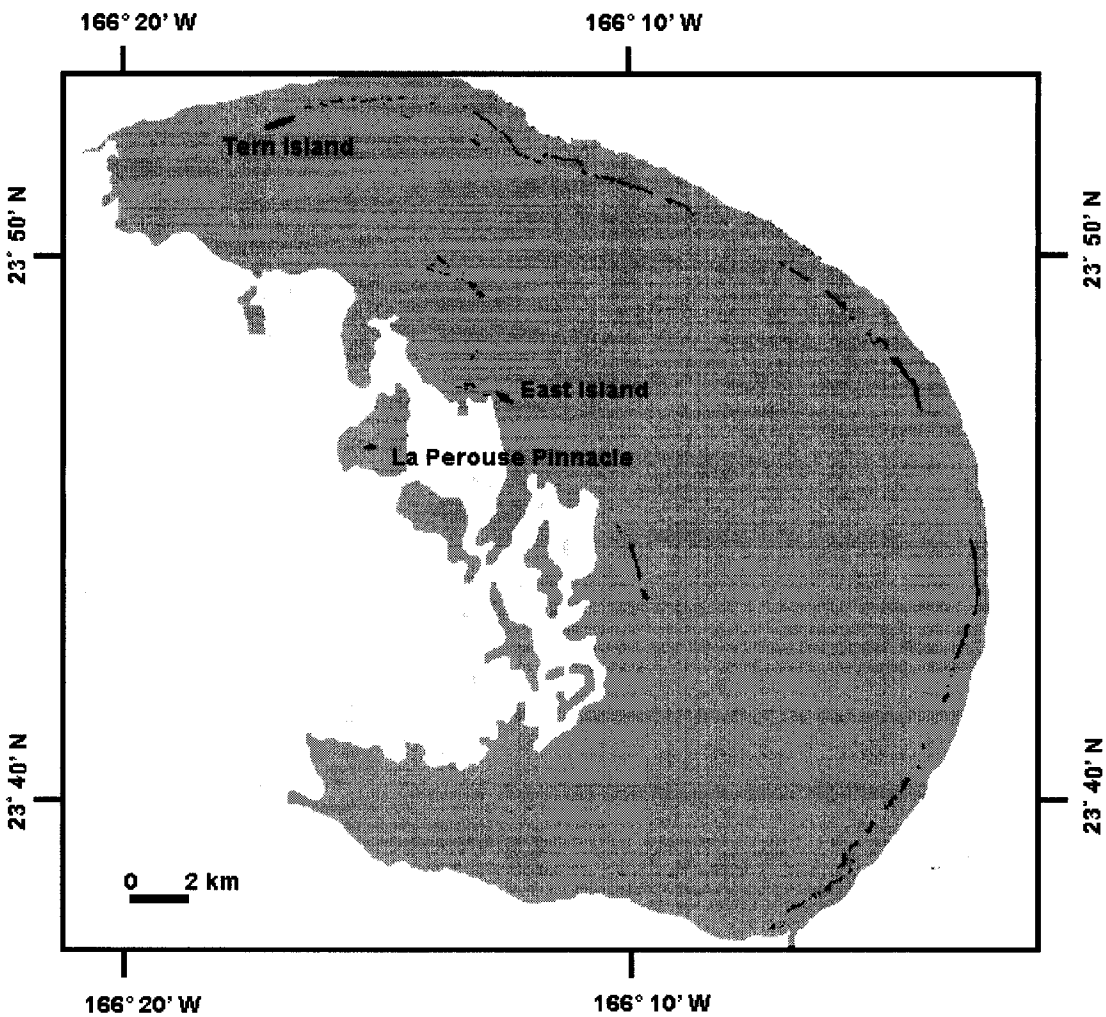

Figure 1.3: French Frigate Shoals, Northwestern Hawaiian Islands

CHAPTER 2

THE BREEDING BIOLOGY OF TRISTRAM'S STORM-PETREL AT FRENCH FRIGATE SHOALS AND LAYSAN ISLAND, NORTHWESTERN HAWAIIAN ISLANDS

ABSTRACT

Aspects of the biology of Tristram's Storm-petrel (*Oceanodroma tristrami*) were quantified on Laysan Island and French Frigate Shoals in the Hawaiian Islands National Wildlife Refuge to provide information for the species' conservation. Tristram's Storm-petrels bred from mid-October until mid-June. The hatching success on Laysan Island was 0.35 (n = 48) and 0.46 (n = 56) in 2004 and 2005 respectively, and for Tern Island it was 0.53 (n = 86) and 0.61 (n = 34) in 2005 and 2006 respectively. Laysan fledge success was 0.45 (n = 56) and an overall breeding success of 0.16 (n = 50) in 2004. Tern Island experienced a mean fledge successes of 0.51 (n = 45) and 0.47 (n = 19) for an overall breeding successes of 0.27 (n = 85) and 0.28 (n = 32) in 2005 and 2006 respectively. Abandonment rate was high in all years and locations, however, no relation was found between abandonment and frequency of nest site visitation. The next most important factors impacting breeding success after abandonment were nest site competition with larger burrowing seabirds and weather effects. The low annual reproductive rate, found in this study, suggests that Tristram's Storm-petrel may be susceptible to population declines. Further research into demography and aspects of basic biology including foraging niche are required.

2.1 INTRODUCTION

The most massive of the storm-petrels (up to 112g, Marks and Leasure 1992), Tristram's Storm-petrel (*Oceanodroma tristrami*) breeds only in the Northwestern Hawaiian Islands (USA) and the Ogasawara archipelago (Japan). The biology of storm-petrels is known mostly from studies of a few high latitude species (e.g., Leach's Storm-petrel, *Oceanodroma leucorhoa*, and Wilson's Storm-petrel, *Oceanites oceanicus*; Brooke 2004). Tristram's Storm-Petrel belongs to a small group of very poorly known tropical species in the genus *Oceanodroma*. The aim of this study was to elucidate the basic biology of this unusual species.

Likely never one of the more abundant seabird species in the Northwestern Hawaiian Islands, Tristram's Storm-petrel was apparently extirpated from Midway (Fisher and Baldwin 1946, Harrison 1990) and Kure (Rauzon et al. 1985) atolls by invasive rats (Black rat, *Rattus rattus* and Polynesian Rat, *Rattus exulans,* respectively) and has yet to re-establish colonies since rat removal in the late 1990's (B. Flint, C. Vanderlip personal communication), though one recent breeding attempt was recorded at Midway (Baker et al. 1997). Tristram's Storm-petrel was also once extirpated from several islands at French Frigate Shoals by human activity (Amerson 1971), though these islands have since been re-colonized. In other parts of Tristram's Storm-Petrel's range, invasive mammalian predators (Black rat, Siberian Weasel *Mustela sibirica,* and Domestic Cat *Felis catus*; Stattersfield et al. 1998) now limit breeding in the Ogasawara archipelago to mostly small predator-free islets including Tadanaejima and Onbasejima off Kozushima (Slotterback 2002) and Kojine off Hachijo of the Izu Islands (F. Sato personal observation), Kitanoshima of the Ogasawara (Bonin) Islands (F. Sato personal

observation), and Nishinoshima (Kawakami et al. 2005) and Kitaiwojima of the Volcano Islands (Ornithological Society of Japan 2000). The large colony once present on Torishima has been reduced to approximately 150 pairs by black rat predation (F. Sato unpublished), though a rat eradication program is currently in progress.

Despite being considered as near threatened (Birdlife International 2005) and a species of conservation concern (U.S. Fish and Wildlife Service 2002a), Tristram's Storm-petrel remains one of the least studied seabirds in the Hawaiian archipelago, if not the northern hemisphere. Basic information concerning its breeding biology and population status is lacking. Breeding biology has been studied at a single colony (Marks and Leasure 1992) and suffered high abandonment rates and therefore small sample sizes. With the exception of Pearl and Hermes Reef (Wegmann and Kropidlowski 2002) all population estimates of Tristram's Storm-petrel in Hawaii were based on brief visits to islands during the 1980s (see Rauzon et al. 1985). This study was undertaken to address the current lack of breeding biology information available for this species, with emphasis on breeding success and sources of breeding failure at two representative breeding sites. Measurements of adult birds from Tern Island are also presented, as morphometric information are also lacking in the literature.

2.2 MATERIALS AND METHODS

2.2.1 Study area

Observations were conducted at Laysan Island (25°46 N, 171°03' W) and French Frigate Shoals (Tern and East Islands, 23°45' N, 166°10' W) in the Hawaiian Islands National Wildlife Refuge. Located 1495 km northwest of Honolulu, Laysan is a 397 ha

coral sand island featuring a 70 ha hypersaline lake in the centre. Once left completely void of vegetation by introduced European rabbits (*Oryctolagus cuniculus*) (Ely and Clapp 1973), Laysan is in the midst of an island restoration project undertaken by the U.S. Fish and Wildlife Service. In 2004, approximately 217 ha, or 66% of available area, was vegetated (McClelland unpublished). On Laysan, Tristram's Storm-petrel is limited to small, scattered sub-colonies (Ely and Clapp 1973) in a 50-250m band of vegetation around the perimeter of the lake basin (Marks and Leasure 1992), the largest located at the southwest corner of the lake. Vegetative community of sub-colonies differs greatly, ranging from open areas with sparse bunchgrass (*Eragrostis variabilis*), to dense vines (*Ipomea pes-capae*, *Sicyos pachycarpus*).

French Frigate Shoals is a crescent-shaped coral atoll located 540 km southeast of Laysan Island and 955 km northwest of Honolulu. Of the 12 to 16 coral sand islets present at any given time, only Tern and East Islands currently support vegetation and appreciable burrowing seabird populations. Tern measures 13.8 ha (U.S. Fish and Wildlife Service 2002b) and East 4.5 ha (Amerson 1971) respectively, though this study found Tristram's Storm-petrels use only 0.1 ha on Tern and 0.8 ha on East for breeding. Tristram's Storm-petrel began re-colonizing Tern in 1993 (U.S. Fish and Wildlife Service unpublished) and East by no later than 1985 (Rauzon et al. 1985).

Activity at Tristram's Storm-petrel breeding sites was quantified from November 2003 to June 2004 and October 2004 to April 2005 on Laysan Island and from December 2004 to June 2005 and January 2005 to June 2006 at French Frigate Shoals. Measurements of Tristram's Storm-petrel adults on Tern Island were taken from March 14th to March 27th, 2006.

2.2.2 Tristram's Storm-petrel Nest Site Monitoring

All breeding sites were located and monitored in the daytime with the use of a 2.5 cm diameter infrared video probe (Peep-a-roo, Sandpiper Technologies, Inc.). Storm-petrels can be negatively affected by researcher disturbance (Blackmer et al. 2004, Boersma et al. 1980, Wilbur 1969) and Tristram's Storm-petrel may be especially susceptible (Marks and Leasure 1992). Therefore, to keep disturbance to a minimum, at no time were adults handled or touched. Presence of an egg was inferred by the presence of an adult in incubating posture over a central nest cup at a breeding site for three consecutive nest checks over a 10 to 12 day period. Breeding sites were monitored at 4-day intervals in 2004 but decreased to once every 7 days during the incubation stage on Laysan in 2005 and Tern Island in 2005 and 2006. Due to logistical constraints, sites at East Island, French Frigate Shoals were monitored only in 2005, approximately every 21 days.

2.2.3 Nest Site Characteristics

Nest site measurements were only taken on Laysan. Recorded for each nest was structure (earthen burrow, vegetation, or rock crevice), entrance width and height, burrow length, and whether a curve (in the entrance tunnel) was present. Burrow sites were identified by having a tunnel and nest cup surrounded by earth only. Vegetation sites were identified as an aboveground nest cup sheltered by a dense covering of vegetation. Rock crevice sites were identified as a nest cup accessible through an opening between

rocks and surrounded by rock only. Temperature was recorded every one minute in a small sample of occupied burrows on Laysan with the use of Stowaway TidbiT Temp Loggers (Onset Computer Corporation). To ensure that air and not soil temperature was recorded, loggers were suspended in small wire cages and placed in the back of the burrow behind the nest bowl. To avoid disturbance, no loggers were placed in active burrows with incubating adults. Daily minimum and maximum outside ambient air temperatures were measured with a wet/dry thermometer placed in a Stevenson Screen located 1 km from the study site.

2.2.4 Breeding Biology

All dates referring to the species' phenology were calculated using the median of the earliest and latest dates possible based on nest checks. Nests that were potentially already being incubated when first recorded were excluded from calculations of hatch period. Because Tristram's Storm-petrels likely do not brood their chicks for more than 2-3 days after hatching (Marks and Leasure 1992), hatch date was assumed to be at least 2 days prior to when the chick was first observed unattended. Chicks were assumed to have fledged if they were fully feathered and at least 70 days old prior to when the empty nest was recorded.

Tristram's Storm-petrels do make use of artificial nest boxes on Laysan and Tern (McClelland, ms. in preparation). These nests were included in estimates of phenology, population, and hatch and fledge periods but excluded from estimates of hatch and fledge success because they are exempt from sources of nest failure such as burrow collapse that natural nest sites experience.

Hatch success was calculated as the proportion of eggs that successfully hatched among those laid. Fledge success was calculated as the number of chicks that fledged among eggs hatched for Tern Island. Because of a very small sample size on Laysan in 2004, chicks that were found within an estimated 14 days of hatch were included in fledge success but excluded from hatch success and fledge period. Breeding success was calculated as hatch success times fledge success.

2.2.5 Nest Failure due to Bonin Petrel or Wedge-tailed Shearwater

Bonin Petrel (*Pterodroma hypoleuca*) interference involved either annexation of a Tristram's Storm-petrel nest site by ejection of the occupying adult or the collapse of a Tristram's Storm-petrel burrow caused by a Bonin Petrel digging a burrow of its own. An annexation occurred when a Tristram's Storm-petrel was immediately replaced by a Bonin Petrel or if a Tristram's Storm-petrel abandonment coincided with the enlargement of the original burrow and later occupation by a Bonin Petrel within two nest checks. Only confirmed breeding sights were included.

Direct Wedge-tailed Shearwater (*Puffinus pacificus*) interference involved Tristram's Storm-petrel chick mortality from killing or eviction. A mortality was indicated by a chick found dead at the entrance of the nest site with physical trauma. An eviction was indicated by either a live chick at the entrance to the burrow or a missing chick that coincided with a Wedge-tailed Shearwater occupying the original nest site. Indirect mortality was indicated by the loss of a nest site due to digging activity: either entombment by blockage of the entrance sufficiently to prevent Tristram's Storm-petrel adults from leaving, or by causing a burrow collapse.

2.2.6 Adult and Chick Measurements

Adult and chick measurements were collected at Tern Island in 2006. Adults were captured at night on the surface. Body mass (± 1 g using a 300 g Pesola spring balance) and wing chord (± 1 mm using a stopped ruler) were measured for both adults and chicks, and included culmen and tarsus length (± 0.1 mm with slide callipers) measurements for adults. The logistic growth constant for chicks was calculated using logistic growth curves (Ricklef's 1967) fitted to each chick's body mass measurements only up to peak mass, using only chicks of known age that survived to fledge.

2.2.7 Population Estimates

Population estimates based on numbers of active breeding sites present were derived for both islands. On Laysan, a breeding population estimate was made based on the average observed burrow density of the southern sub-colony applied to the estimated area of additional sub-colonies. Tern Island is small enough to allow census through direct count of all sites and the island was surveyed twice over the course of the 2005 breeding season. East Island was also surveyed in 2005, however, a direct count of Tristram's Storm-petrel burrows was not possible due to the infrequent and relatively short duration of visits to the island. Instead, the colony was divided into 10 m wide strips that spanned its width. Direct counts of burrows were conducted in every other strip and the number of occupied burrows present in the unsurveyed strips was estimated using the average burrows/ha of the two adjacent strips.

2.2.8 Statistical Analyses

Statistical analyses were performed using Minitab, Release 13 (Minitab Inc. 2000). Binomial logistic regression models with a logit link function were used to analyse relationships between nest success and nest site characteristics, lay date, monitoring frequency, and burrow collapse (Hosmer and Lemeshow 1989). The same models were also used to test the relationship between annexation by Bonin Petrel and Wedge-tailed Shearwater and Tristram's Storm-petrel nest sight characteristics and location. All results were considered significant when $p \leq 0.05$. Values reported in the Results section are means ± SD. Relevant statistical models are presented in Appendix III.

2.3 RESULTS

2.3.1 Breeding Site Characteristics

Breeding site types present on Laysan included earthen burrows, vegetation sites and rocky crevices (74%, 17%, and 10% respectively, $n = 115$). The Tristram's Storm-petrel colony sites in French Frigate Shoals lacked rocky crevices and dense vegetation and all breeding sites were located in earthen burrows, under or near beach heliotrope (*Tournefortia argentea*) on Tern Island, and among herbaceous plants such as nettleleaf goosefoot (*Chenopodium murale*) on East Island, which lacks beach heliotrope in the colony site. Burrow entrances measured 8.9 ± 2.4 cm wide and 5.5 ± 1.7 cm high ($n = 42$) in January 2004 but 10.3 ± 4.8 cm wide and 7.0 ± 2.5 cm high ($n = 48$) in January

2005. Burrow length was highly variable (36.6 ± 15.3 cm, range = 15 - 70, n = 42) with 50% curving left or right (n = 82). No relationship was observed between hatch or fledge success and burrow characteristics, though the sample size did not allow for a test of the significance of interaction terms.

On all three islands burrows were often established where an object such as a plant root or tussock could provide increased stability to the entrance. Burrows were constructed shallow enough to allow adults to extricate themselves in the event of a collapse and associated adult mortalities were extremely low (<1% of all burrows, n = 218, or 11% of all collapses during incubation stage, n = 18). Tristram's Storm-petrel occasionally located their burrows under or within close proximity to albatross nest mounds. It is not known if these burrows experienced lower hatch success but they did often suffer heavy alteration, as albatross may remove soil from the entrance while grooming and adding to the mound, shortening the burrow up to 15 cm in one instance. Tristram's Storm-petrel also established breeding sites in nest boxes or under man-made debris if available.

Occupied burrow density at the southern end of the lake on Laysan averaged 0.025/m^2 but reached as high as 0.105/m^2 in some locations. Average occupied burrow density on Tern and East was 0.111/m^2 and 0.028/m^2 respectively. A total of 86% of burrows on Tern Island in which an adult was observed eventually became an active breeding site.

Average temperature was 24.1 ± 1.3 ° C in earthen burrows (n = 3) and 23.2 ± 1.6 ° C in vegetation breeding sites (n = 2). Average fluctuation in temperature over a 24-hour period was 0.5 ± 0.4 ° C (n = 3) and 2.8 ± 1.6 ° C (n = 2) in earthen burrows and

vegetation breeding sites respectively. Though vegetation breeding sites often achieved higher temperatures in the day, they were less insulated and lost heat much quicker at night, dropping to within 3.3 ± 1.0 ° C of the ambient air temperature compared to earthen burrows that maintained an average 5.2 ± 1.3 ° C above ambient air temperature (Figure 2.1).

2.3.2 Breeding Phenology

By late October large numbers of adults were on the ground surface at night at the colony sites and burrows were occupied in the daytime. Vocal displays on and over the colony site were frequent initially, but calling behaviour noticeably decreased in late December with the onset of incubation. First egg was laid in early December (December 7th to 18th) and the first chicks appeared within the last two weeks of January (January 21st to February 1st). Non-breeding adults noticeably increased in mid-February with individuals or pairs occupying burrows during the daytime and vocalizations were again common. Last hatch occurred mid-March, with the first fledglings in mid April (April 15th to 20th). By mid-June all chicks had fledged and the colonies were again empty (June 10th to 15th).

Breeding within colonies was highly synchronized (Figure 2.2). Phenology between islands did not appear to differ between years and the timing on Laysan closely matched the 1988 and 1990 breeding seasons described by Marks and Leasure (1992). Between locations, French Frigate Shoals was consistently 7 to 8 days earlier than Laysan in terms of first and last egg, hatch, and fledge. However, with birds breeding in nest

boxes on Tern excluded, there was little difference in phenology between islands (Table 2.1).

2.3.3 Incubation Period and Hatch

Eggs on Laysan measured 39.3 ± 1.1 mm, by 28.8 ± 0.3 mm with a mass of 18.2 ± 0.8 g (n = 4). Incubation period is available from only Tern Island in 2005, lasting 44.5 ± 5.3 days (range = 39 - 55, n = 21). One nest was incubated for 64 ± 6 days before being abandoned. A possible case of egg replacement was recorded but could not be confirmed, as individuals could not be identified.

Laysan Finches (*Telespiza cantans*) were effective egg predators, depredating 90% of all unattended eggs within 2-4 days (n = 21) and no egg survived unattended beyond 8 days. Despite this fact egg neglect was observed in 10% (5) of nests on Laysan in 2004 (n = 48). Of those nests, two were in nest boxes, which finches appeared reluctant to enter, for a total of 33% of breeding pairs in nest boxes practicing the behaviour (n = 6). A third nest was in a rock crevice that was likely inaccessible to finches. Egg neglect was not recorded on either Laysan in 2005 or French Frigate Shoals in 2005 or 2006 (n = 56, 114, and 51 respectively)

Laysan Island experienced a hatch success of 0.35 (n = 48) and 0.46 (n = 56) in 2004 and 2005 respectively, while Tern Island experienced a success of 0.53 (n = 86) and 0.62 (n = 34) in 2005 and 2006 respectively. East Island had a hatch success of 0.54 (n = 28) in 2005. No detectable relationship between hatch success and lay date was found in any breeding season. Researcher disturbance did not appear to be a factor in hatch success as there was no significant difference between nests that were checked every 4

(Laysan 2004), 7 (Laysan 2005 and Tern 2005, 2006), and 21 days (East 2005) when controlled for other known sources of failure ($G = 4.401$, $p = 0.11$, $n = 169$). Nor did the rate of abandonment differ significantly between years on Laysan ($G = 1.714$, $p = 0.19$, $n = 82$), or between islands at French Frigate Shoals ($G = 0.023$, $p = 0.88$, $n = 87$).

Sources of nest failure were numerous and varied between islands (Table 2.2). Bonin Petrels annexed only burrow nest sites. The petrels ejected Tristram's Storm-petrel by using their size advantage to force themselves in behind the incubating Tristram's Storm-petrel and forcing it and it's egg out of the nest bowl. Broken or cracked Tristram's Storm-petrel eggs were found in recently annexed burrows on Laysan, though it is not known if the egg was purposely damaged by the Bonin Petrel or as a result of fighting between the two species. In one instance where the egg was not damaged, the Tristram's Storm-petrel continued to incubate the ejected egg beside the nest bowl along side the Bonin Petrel for several days before abandoning. No significant relationship was found between Bonin Petrel annexation and nest site characteristics or location.

A heavy rain event in December accounted for the largest percentage of all failed nests on Tern Island in 2005. Laysan and East also experienced this event, but because surveys had yet to begin, the number of failed nests is unknown. Therefore, Laysan and East likely suffered lower hatch success in 2005 than indicated. It is likely Laysan especially suffered high breeding failure, as the southern end of the lake, where the highest densities of storm-petrels were found, was flooded for several weeks.

2.3.4 Nestling Period and Fledge

Average nestling period was 83.8 ± 2.0 days (n = 5) on Laysan in 2004 and 83.7 ± 4.7 (n = 20) and 87.1 ± 6.8 (n = 15) on Tern Island in 2005 and 2006 respectively. Chicks were recorded as fledging as young as 74 days (Tern Island 2005), and as old as 100 (Tern Island 2006). Chicks reached a peak mass of 139.7 ± 10.2 g and fledged at 96.9 ± 9.6g (n = 14) (Figure 2.3). The body mass of Tristram's Storm-petrel adults is known to decrease as the breeding season progresses (Marks and Leasure 1992), but prelaying body mass is unknown. Using the earliest seasonal value available (February, Marks and Leasure 1992), chicks peak at 150% of average adult mass and fledge within 4%. The logistic growth constant was 0.101 ± 0.008 (n = 12), with chicks requiring an average of 43.5 days to grow from 10% to 90% asymptotic mass. These values correlate closely with those from Marks and Leasure (1992), though it should be noted methodologies differ.

Fledge and overall breeding success was available for only Laysan in 2004 and Tern Island in 2005 and 2006. Laysan experienced a fledge success of 0.45 (n = 56) and an overall breeding success of 0.16 (n = 50). Tern Island experienced fledge successes of 0.51 (n = 45) and 0.47 (n = 19) for overall breeding successes of 0.27 (n = 85) and 0.28 (n = 32) in 2005 and 2006 respectively. The sporadic monitoring of East Island in 2005 did not allow an accurate assessment of fledge success but could be no more than 0.40 (n = 15), for an overall breeding success of less than 0.22 (n = 28).

Sources of chick mortality were similar between islands but the importance of a specific source varied greatly (Table 2.3). Tristram's Storm-petrel chicks that were found missing were assumed to have permanently left their nest site on their own. In one

instance a chick went missing for 14 days before returning to its original burrow. During this time it likely occupied a nearby burrow (1 m distance) that was inaccessible to the researcher. It later fledged at the expected age, though it is unknown if it was fed during this period. All other chicks that were found in second burrows and failed to return to their original did not survive beyond a maximum of 15 days (n = 6). This includes 3 burrows already occupied by smaller Tristram's Storm-petrel chicks.

Direct Wedge-tailed Shearwater interference on Tern Island was rare, as no chicks were killed and only one eviction was recorded in each breeding season. In addition, in 20% and 33% of nest sites in 2005 and 2006 respectively, Wedge-tailed Shearwaters were witnessed sharing burrows with Tristram's Storm-petrel chicks for periods of several days, in one instance being present for five consecutive nest checks over a 24-day period. On two occasions Wedge-tailed Shearwaters were observed preventing the feeding of Tristram's Storm-petrel chicks by blocking the burrow entrance from the adult. This was not an aggressive defence of the burrow and Tristram's Storm-petrel adults were not observed attempting physical contact with the much larger shearwaters, nor could vocalizations be heard, though any would have been lost in the noise of the large population of Sooty Terns (*Sterna fuscata*) that share the colony. The fledge success of chicks which shared burrows with Wedge-tailed Shearwater did not differ significantly from chicks that did not. No significant relationships were found between annexation by Wedge-tailed Shearwater and nest site characteristics or location.

One chick on Laysan was lost to invasive arthropods (see Chapter 4). Invasive ants (*Monomorium pharaonis* L.) dominate Laysan and were occasionally witnessed harassing chicks. This included ants massed around the chick's head and cloaca with the

chick demonstrating foot-stomping behaviour and an inability to sit still. One chick was found obviously harassed on several occasions and was found missing directly following a strong harassment event involving approximately 200 ants. Because the chick's disappearance coincided with a strong harassment event, invasive ants are considered implicit in the chick leaving the nest and the associated mortality.

2.3.5 Adult Measurement

The mean body mass of 27 adults was 92.1 ± 8.0 g (range = 78 - 110g). Means of other measurements include: wing chord, 183.3 ± 4.0 mm (range = 177 - 191); culmen, 18.9 ± 0.7 mm (range = 17.5 - 20.7), and tarsus length, 27.4 ± 1.2 mm (range = 25.5 - 29.9). One captured adult was missing a foot. A bird banded on Tern Island as a chick in 2002 was captured at the mouth of an active burrow on Tern (March 21st, 2006), but could not be confirmed as a breeder.

2.3.6 Population Estimates

The Laysan population of Tristram's Storm-petrel was estimated to be 700 breeding pairs. Applying the average density of the largest colony to the estimated amount of suitable habitat, the population cannot exceed 2250 breeding pairs. The Tern Island population was found to be at least 112 breeding pairs but likely does not exceed 120. The East Island population was estimated to be at least 140 breeding pairs, and was likely 160 pairs assuming that only 89% of all nests had been initiated at the time of the

survey, as they had on Tern. The estimate does not account for nests that may have failed prior to the survey, making 140-160 breeding pairs a conservative population estimate.

2.4 DISCUSION

This study provided new data on the breeding biology of Tristram's Storm-petrel and adds to the existing information from Hawaii and elsewhere all of which expands our understanding of this obscure species. Anecdotal evidence (Rauzon et al. 1985) suggested there may be geographic variation in Tristram's Storm-petrel phenology, with breeding occurring earlier on more eastern islands in the Northwestern Hawaiian Islands archipelago such as Nihoa. A similar pattern has been documented in other species with highly synchronized colonies such as Sooty Terns (Fefer et al. 1984). Nevertheless, little difference in phenology was found between French Frigate Shoals and Laysan Island in 2005, but the possibility requires further study over a greater geographical range. Breeding pairs using nest boxes on Tern bred earlier than birds that dug burrows. Tristram's Storm-petrels on Nihoa Island take advantage of loose rock (Rauzon et al. 1985), which also precludes the need to dig burrows, and may also help explain observed differences between islands. The presence of the world's largest colony of Bulwer's Petrel on Nihoa (Megyesi and O'Daniel 1997) may also exert selection pressure towards earlier breeding as there is speculation the summer-breeding Bulwer's evict Tristram's Storm-petrel chicks from breeding sites upon arrival (Harrison 1990).

Members of the genus *Oceanodroma* are predominantly summer breeders, with the exception of Tristram's Storm-petrel, some populations of the Band-rumped (Madeiran) Storm-petrel (*Oceanodroma castro*; Monteiro and Furness 1998), and the

Guadalupe population of Leach's Storm-petrel (Ainley 1980). Though present at breeding sites by January (Enticot and Tipling 1997, Harrison 1985), Matsudaira's Storm-petrel likely initiates egg-laying in late March (F. Sato personal observation), three months after Tristram's. The timing of birds' breeding seasons is supposed to coincide with maximum food resource availability for the young (Lack 1968). Monteiro and Furness (1998) speculated that the Azores (38° N) population of the Band-rumped Storm-petrel preferred to breed in the winter because of the increased feeding opportunities on vertically migrating mesopelagic lantern fish associated with the increased advection of mesopelagic prey from higher surface winds, and a longer period of darkness in which to exploit this prey. It is possible the breeding season of Tristram's Storm-petrel is timed for the former advantage. At only 23° N, there is little difference between summer and winter day lengths in Hawaii. The foraging ecology of Tristram's Storm-petrel is virtually unknown and sole source of information was 10 well-digested regurgitation samples collected from two islands from 1979-81 (Fefer et al. 1984). In addition, the at sea distribution and foraging range is poorly understood (Slotterback 2002), making speculation on the ecological niche difficult. However, members of the mesopelagic fish family Sternoptychidae represented a large percentage (by volume) of identifiable remains (23%, second only to squid of an unknown family at 29%) in collected samples (Harrison et al 1983). Another species in the archipelago that is highly reliant on mesopelagic fish and squid is the Bonin Petrel (Seto and O'Daniel 1999). Given this species has a breeding season that strongly overlaps that of Tristram's Storm-petrel (Figure 2.4), it is tempting to conclude that Tristram's Storm-petrel breeds in winter to exploit a prey resource similar to that of Bonin Petrel, though some form of resource

partitioning would be almost certain considering the morphological differences between the two species.

Tristram's Storm-petrels on Laysan showed a strong preference for burrow nesting sites but it should be noted that the vegetation sites were extremely cryptic and likely more common than detected by us. In some areas of Laysan, Tristram's Storm-petrel may also establish burrows in areas dominated by thick vines (Marks and Leasure 1992) but these sites were not studied or surveyed due to the likely high level of investigator disturbance.

Tristram's Storm-petrels excavated their own burrows over a period of several weeks. As found in other species of storm-petrel (Stenhouse and Montevecchi 2000, Harris 1974), soil type was a large factor in colony location. Tristram's Storm-petrel preferred shallow, less sandy soils that likely offer greater burrow stability and suffer less competition from Bonin Petrels and Wedge-tailed Shearwaters, which prefer deeper soils (Ely and Clapp 1973). It was not know if constructing shallow burrows was a strategy employed in response to the common collapses suffered in the sandy soils of the Northwestern Hawaiian Islands or more reflective of the limited digging capabilities of such a small bird in sandy soils. For example, Bonin Petrel and Wedge-tailed Shearwater dig much deeper and more stable burrows.

The difference in burrow entrance size between years on Laysan was likely due to a heavy rain event that occurred prior to measurements in 2005. Erosion appeared to increase burrow diameter over the course of the breeding season and minor entrance collapses were common, in some cases completely blocking the entrance. In most instances adults continued to incubate until excavated by the other member of the pair, on

one occasion remaining entombed for 3 to 5 days. Marks and Leasure (1992) suggested that the high abandonment rate observed in their study was due to minor alterations to the burrow by investigator activity that the bird might perceive as an indication that the burrow was unstable and therefore unsafe. However no relationship between burrows that suffered a minor collapse and increased abandonment rate was found on Tern Island, the only island for which minor collapses were consistently recorded.

The highest occupied burrow density recorded in what was presumably the most desirable habitat on Laysan corresponded closely with the average on Tern. In many storm-petrel colonies the substrate is stable enough that burrows are not in danger of collapsing if another burrow intersects with it, allowing for densities as high as $3.1/m^2$ (Huntington et al. 1996). This is not the case on coral sand islands where burrows, at least as shallow as those of Tristram's Storm-petrel, likely do not survive interference from other burrowing seabirds. It is likely the densities recorded on Laysan and Tern Island represented the maximum possible given the substrate, in which case the Tern Island colony is close to maximum carrying capacity.

The costs associated with incubation have the potential to increase mortality in adult birds (Visser and Lessels 2001) and there is a greater fitness benefit to reducing risk of adult mortality than increasing fecundity in species with high adult survival (Barbraud and Weimerskirch 2001). As a result, egg neglect evolved in petrels to allow adults to maintain a high level of fitness (Boersma and Wheelwright 1979) and limit incubation-induced adult mortalities. It was extremely difficult to speculate on the true incidence of egg neglect by Tristram's Storm-petrel on Laysan, as the percentage of eggs considered abandoned that would have continued to be incubated had the egg not been depredated

cannot be known. However, the fact the species continues to practice egg neglect despite being subjected to Laysan Finch egg predation for untold generations suggests finch egg predation did not affect breeding success to a degree that the benefits of egg neglect were lost.

The greatest cause of hatch failure for all years and islands was abandonment. Abandonment is a common cause of egg loss in Procellaridae (Warham 1996), though what factors contributed to the high rate during this study are unknown. The frequency of the breeding site checks did not appear to significantly affect the abandonment rate of this species based on the results of this study, though comparisons between nests on the same island during the same year would be required for a more rigorous test. If researcher disturbance was indeed not an issue, the abandonment rate may have been reflective of foraging conditions or some other unknown factor.

Other sources of failure varied greatly between islands. Though a feature on all islands, collapses were the greatest source of hatch failure on East Island. East has noticeably coarser soil than the other islands and this was likely the greatest contributor to the high level of collapse. East has the largest population of breeding Hawaiian Green Sea Turtles (*Chelonia mydas agassizii*) (Balazs and Chaloupka 2004) but they were not found to venture into the Tristram's Storm-petrel colony site during the storm-petrels' winter - spring breeding season and thus were not considered a factor.

The denizens of the large Bonin Petrel colony on Laysan were the greatest source of storm-petrel hatch failure on that island. The percentage of nests lost to Bonin Petrel in this study accounted for only Tristram's Storm-petrel nests that could be verified by either three consecutive nest checks or the presence of an egg after abandonment.

Therefore these percentages represent the minimal level of Bonin Petrel interference and the actual level is possibly much higher. As mentioned above, there is a strong overlap between the Tristram's Storm-petrel and Bonin Petrel breeding seasons. On islands with large populations of Bonin Petrel such as Laysan, large numbers of each species are prospecting and competing for burrows during the same period. The large effect of Bonin Petrel on nesting success may explain why Tristram's Storm-petrel has yet to be recorded breeding on Lisianski Island which has approximately 4.5 times the density of Bonin Petrels than Laysan (calculated from Fefer et al. 1984). This also corresponds with the relatively large population of Tristram's Storm-petrel at Pearl and Hermes Reef, which lacks a large Bonin Petrel presence (Fefer et al. 1984).

Albatross were also negative factors in Tristram's Storm-petrel hatch success, though only on Laysan was this directly documented. Albatross, specifically Laysan Albatross (*Phoebastria immutabilis*), were witnessed causing Tristram's Storm-petrel burrows to collapse and albatross chicks were frequently attracted to burrow entrances, which they blocked and altered in an attempt to create a new nest bowl (see Rice and Kenyon 1962). Though Tern and East Islands also have high densities of albatross, burrows on Tern appeared to be spared a large amount of interference as the burrows were often situated under beach heliotrope and experienced less bird traffic. East Island was not monitored closely enough to document their effects, though considering the much higher rate of collapse on the island, albatross may have been a factor.

Based on the observations of egg neglect in 2004, Laysan Finches likely decrease Tristram's Storm-petrel hatch success, though as mentioned above, the level of significance is difficult to determine. It cannot be assumed that Laysan Finches have a

negative impact on Tristram's Storm-petrel populations, though their potential impact needs further study and may vary across years as the prevalence of egg neglect may be dependant on foraging conditions (Chaurand and Weimerskirsh 1994).

Though it was not possible to quantify the number of nests lost to flooding on Laysan in 2005, flooding of the southern lake area occurs during heavy rain events (Willet 1919) and is likely a substantial source of nest failure during these years (Ely and Clapp 1973). This is especially true considering the highest densities of Tristram's Storm-petrel were found in this area and the periods of heavy rain are most frequent during the storm-petrel's incubation period. The greater tendency of collapse on East Island may indicate that island's storm-petrel nests are susceptible to the negative effects of weather.

Willet (1919) described sand storms entombing many burrows on Laysan but these events are likely rare as no other mention of this occurrence has been recorded in the literature. The highest densities of Tristram's Storm-petrel burrows are also found in shallow, less-sandy soils and would be the least affected by such an event.

Tristram's Storm-petrel chicks were highly mobile and often moved to the entrance of the burrow to exercise their wings at night. They occasionally left the burrow for short periods of time, sometimes being found absent from burrows only to return a day later. When absent from their natal burrow, chicks made use of nearby burrows and usually returned to their own the following night, likely orienting with olfactory cues (De Leon et al. 2003). The survival of the youngest and original occupying chick in burrows into which an older chick entered and simultaneously occupied is consistent with some level of chick recognition by adults. Chick recognition has also been suggested in the

Wedge-rumped Storm-petrel (*Oceanodroma tethys*), another species with highly mobile chicks (Harris 1969).

Though Wedge-tailed Shearwaters were the greatest single cause of chick loss on both Laysan and Tern, the behaviour and method of mortality varied greatly between islands. The largest of the burrowing birds in the archipelago, Wedge-tailed Shearwaters readily evict other burrowing species (Whittow 1997). On Laysan, shearwaters are aggressive competitors for burrows, arriving and prospecting in March, and often killed and evicted Tristram's Storm-petrel chicks. Why this aggression was absent on Tern Island is puzzling and becomes more so when Bonin Petrels are considered. Wedge-tailed Shearwaters were also aggressive towards Bonin Petrels and contributed to at least 38% (n = 32) of all chick mortalities on Laysan in 2004. Shearwaters annexed all 13 Bonin Petrel nests on Tern Island in 2005 (not including those protected by nest boxes), killing the only known chick at less than two weeks of age. Further investigations into the interactions between these two species and how they differ among islands are required.

Despite the lack of direct interference on Tern Island, Wedge-tailed Shearwaters continued to be a large source of mortality indirectly. The higher incidence of indirect interference on Tern is likely due to the greater burrow density than on Laysan.

Despite speculation by Harrison (1990), no Tristram's Storm-petrel chicks were evicted by Bulwer's Petrel on any island, though Bulwer's Petrels used some burrows after the storm-petrel chick had fledged or the nest had failed on Laysan. It is doubtful that Bulwer's Petrel is a source of chick mortality on these islands as burrows are ephemeral, lasting in most cases one breeding season, and it is unlikely a Bulwer's Petrel

would have such a strong attraction to the burrow to try to kill or evict a well-developed Tristram's Storm-petrel chick that is greater than or close to its own mass (Megyesi and O'Daniel 1997). It is unknown if Bulwer's Petrel has a negative effect on islands such as Nihoa and Necker where Tristram's Storm-petrel nesting may occur in crevices repeatedly used by Bulwer's Petrel pairs. Further research into these interactions is required.

It was not known how large a source of mortality the hypersaline lake on Laysan (and its variation in size by flooding during rainy periods) was to Tristram's Storm-petrel chicks. Several drowned fledglings were found around the lake edge during the course of the breeding season but it is not known what proportion of chicks is lost per year.

Tristram's Storm-petrels breeding on sand islands (Laysan, French Frigate Shoals, Pearl and Hermes Reef, Midway and Kure atolls) must suffer significant annual nest loss to weather effects and the fragility of sand burrows. When coupled with the presence of large populations of Bonin Petrel and Wedge-tailed Shearwater, it is likely Tristram's Storm-petrel rarely achieves a breeding success comparable to other member of its genus. While breeding success of other *Oceanodroma* are frequently above 0.4 (Table 2.4), Tristram's Storm-petrels may loose over 20% to 30% of nests to interspecific competition alone. The only other member of the genus to have a comparable breeding success is the Band-rumped Storm-petrel, which also suffers from competition with larger and aggressive burrow competitors (Ramos et al. 1997).

Tristram's Storm-petrel has the benefit of not suffering from adult predation pressure at breeding sites and adult mortality is likely low. Still, it would appear that their breeding success on Laysan and East might rest dangerously close to the limit of

sustainability. For example, using the formula described by Brooke (2004), if the average age of first breeding is five years as it is for Leach's (Huntington et al. 1996), and the conservative assumption of an annual adult mortality rate of 5% is used, with immatures suffering twice that, Tristram's Storm-petrel must achieve an average breeding success of 0.18 to maintain the population.

The Laysan population estimate of 700 breeding pairs attained in this study appears comparable with previous estimates of 500 to 2500 (Rauzon et al. 1985) and 2000 to 3000 (Ely and Clapp 1973). An estimate of 20,000 by Willet in 1912 "was almost certainly excessive" (Ely and Clapp 1973). Though the largest island in the Northwestern Hawaiian Islands, based on previous observations it is doubtful Laysan was ever a significant population centre for Tristram's Storm-petrel (see Ely and Clapp 1973), nor will it ever be, based on current habitat usage and interspecific competition.

The Tern and East Island populations of Tristram's Storm-petrel in 2005 were estimated to be a combined 252 - 280 breeding pairs. However, one other islet at French Frigate Shoals may also support a Tristram's Storm-petrel population. La Perouse Pinnacle offers habitat in the form of rock crevices, likely similar to those found on Nihoa and Necker Islands. Landings on the island are rare but Bulwer's Petrel was observed to occupy almost every crevice available in late May, 2005. Though only a small portion of the pinnacle was observed, if densities are representative of the entire pinnacle, La Perouse may support a population of several thousand Bulwer's Petrels. It is not known to what extent this translates into suitable Tristram's Storm-petrel habitat, but it is likely La Perouse supports at least a small breeding population. It is doubtful if a safe and accurate survey of Tristram's Storm-petrel could ever be conducted on La

Perouse but it should be considered that one other island in the atoll may support appreciable numbers of this species.

Marks and Leasure's (1992) study constituted the sole research conducted on the breeding biology of Tristram's Storm-petrel prior to this study. Several insights and hypothesis made in their paper can be addressed by the current research.

Marks and Leasure's (1992) nest checks involved grubbing the burrow; either removing and handling adults for 5-8 minutes for banding, weighing, and measuring purposes, or removing eggs to examine them. This led to an abandonment rate of 63% after two rounds of nest checks. They hypothesized that this high abandonment rate was due to alterations made to the burrow as opposed to apparent predation risk, citing the bird's unwillingness to leave the burrow immediately, preferring to wait until dark. Since then, Tristram's Storm-petrel has been considered very sensitive to researcher disturbance, with the possibility of slight burrow alteration enough to cause abandonment. However, based on the lack of correlation between abandonment and burrow entrance collapse in this study, it now appears that the high abandonment rate suffered by Marks and Leasure (1992) was due to the disturbance associated with grubbing the burrow.

Marks and Leasure (1992) also hypothesized that Tristram's Storm-petrel breeding on islands with egg-predating finches practiced egg neglect less often than those on finch-free islands. As recorded in this study, Tristram's Storm-petrel on Laysan do practice egg neglect, and though it is difficult to accurately assess the frequency of this behaviour, it is possibly high in some years. As to testing if egg neglect is more common on finch-free islands, it should be noted that all finch-free islands in the archipelago that

contain Tristram's Storm-petrel colonies, with the exception of Necker, the colonies have either been extirpated at some point in the recent past (French Frigate Shoals, Midway Atoll, Kure Atoll), or have been exposed to finch predation for possibly several generations (Pearl and Hermes Reef). If comparisons are to be made, they should rely on colonies in the Ogasawara archipelago. Marks and Leasure (1992) also suggested that the introduction of Laysan Finches to Pearl and Hermes Reef might have had a detrimental effect on the breeding success of Tristram's Storm-petrel. This appears very possible based on observations.

Tristram's Storm-petrel may reach up to 112g and are on average 60% heavier than the smallest (Ashy Storm-petrel, *O. homochroa*) and 33% heavier than the next massive member of the genus (*O. matsudairae)*, though these estimates may change as more measurements become available (Brookes 2004). Despite this large size difference, Tristram's Storm-petrel maintain an incubation and fledge period very similar to the much smaller *Oceanodroma* species at similar latitudes (Figure 2.5), strongly corroborating Lack's (1968) assertion that incubation and fledge period differ little among families and are independent of body size.

The systematics of *Oceanodroma* are poorly understood but the genus is thought to be paraphyletic (Nunn and Stanley 1998). Genetic analysis has found that Tristram's Storm-petrel is closely related to Leach's Storm-petrel (Nunn and Stanley 1998), though it should be noted that several *Oceanodroma* species were not included in Nunn and Stanley's (1998) study, and Markham's Storm-petrel (*Oceanodroma markhami*) is almost certainly a closer relative to Tristram's (see Sibley and Monroe 1990). Regardless of the exact structure of the phylogenetic tree of *Oceanodroma*, it is likely that Tristram's

Storm-petrel represents an unusual deviation from the ancestral form and has achieved a body mass unprecedented in the genus. Natural selection implies animals evolve to best exploit their environment and ecological niche (Rayner 1988), and numerous examples of the relationship between morphology and foraging ecology have been documented in birds (Krueger 2005, Gonzalez-Solis 2004, Hromada et al. 2003, etc.). It is possible that the large body size of Tristram's Storm-petrel is linked to foraging ecology and is an adaptation to the unpredictable foraging opportunities in tropical seas that are relatively less productive compared to higher latitudes (Balance and Pittman 1999). Large diet diversity and opportunistic feeding is a common trend in seabirds in the archipelago (Harrison et al.1983). Being larger may allow Tristram's Storm-petrel to capture larger prey and increase its foraging niche, as body size is often the most reliable indicator of prey size in birds (Hespenheide 1973). A broader foraging niche would be especially advantageous as it would make Tristram's Storm-petrel less susceptible to periods of poor foraging. In addition, increased body size means a lower metabolic rate (Kleiber 1947), another advantage during poor foraging conditions. Decreased metabolic rate would also be a especially advantageous during the breeding season as it would allow for longer foraging trips since adults could sustain longer incubation shifts and chicks could tolerate longer periods without being fed. As previously mentioned, speculation on the exact nature of the foraging niche of Tristram's Storm-petrel is extremely difficult. Moreover, there is a lack of life history information such as at sea distribution, length of incubation shifts and chick feeding frequency and morphometrics such as wing loading and aspect ratio. Research into these aspects of Tristram's Storm-petrel biology could provide valuable insight into the evolution of this unique species.

This study demonstrates the need for continued research and monitoring on this poorly understood species. Based on the results of this study, Tristram's Storm-petrel may have a low annual reproductive rate that borders the level of sustainability unless adult mortalities are exceptionally low. Greater research is required to determine if the breeding seasons in this study are representative breeding years. Sources of breeding failure observed during this study also require further investigation in order to gauge their magnitude. Do poor foraging conditions lead to greater occurrences of egg neglect and subsequently high egg loss to finches? Is the lack of aggression from Wedge-tailed Shearwaters on Tern Island normal behaviour on this island, or are the events of 2005 and 2006 unique and Tristram's Storm-petrel suffer higher mortality rates in most years? In addition, the unique characteristics of each island have been shown to have significant effects on Tristram's Storm-petrel breeding success and illustrate the danger of inferring the productivity of one colony based on another. Further research on other islands is needed, especially on non-sand islands that may experience much different breeding conditions. For example, do Tristram's Storm-petrels breeding on Nihoa experience greater nesting success because they nest in rocky crevices and are spared collapses and interactions with Bonin Petrel or are these benefits negated by interference from Nihoa Finches (*Telespiza ultima*) and Bulwer's Petrel?

In addition, many life history characteristics required for the conservation of this species remain poorly understood. Tristram's Storm-petrel demography is incompletely known, lacking basic knowledge such as annual adult survival and age of first breeding. Many aspects of basic biology including foraging niche also require further study. Population levels remain poorly understood and priority must be given to reassessing the

population levels of known colonies and confirming the presence or absence of colonies on Midway Atoll, Kure Atoll, and Lisianski Island. Without further research and monitoring, further declines in Tristram's Storm-petrel will go unnoticed and the abilities to ensure the conservation of this species will be extremely limited. Tristram's Storm-petrels also appear uniquely adapted for their environment. Further research into factors affecting the morphology and current breeding phenology of this species could provide insight into the evolution of not only this species, but its foraging guild as well and should be strongly encouraged.

Table 2.1: Comparison of Tristram's Storm-petrel phenology between years, islands, and natural burrows verses nest boxes in the Northwestern Hawaiian Islands.

	Laysan 2004	Laysan 2005	Tern 2005		Tern 2006	
	Natural Burrows	Natural Burrows	Natural Burrows	Nest Boxes	Natural Burrows	Nest Boxes
First Egg	Dec 15	Dec 14	Dec 13	Dec 07	Dec 19	Dec 11
Last Egg	Mar 03	Unknown	Feb 14	Jan 07	Feb 20	Jan 10
First Hatch	Jan 29	Feb 01	Jan 27	Jan 21	Feb 2	Jan 24
Last Hatch	Mar 17	Mar 21	Mar 10	Feb 27	Mar 5	Feb 9
First Fledge	Apr 20	Unknown	Apr 17	Apr 15	Apr 30	Apr 18
Last Fledge	Jun 15	Unknown	Jun 10	Apr 30	Jun 09	Apr 30

Table 2.2: Sources of hatch failure of Tristram's Storm-petrels at Tern and Laysan Islands, Northwestern Hawaiian Islands

	Laysan 2004	Laysan 2005	Tern 2005	Tern 2006	East 2005
Abandoned	58%	50%	43%	77%	46%
Collapse	13%	10%	10%	33%	54%
Researcher Disturbance[†]	3%	7%	3%		
Rain		*	30%		*
Infertile Egg	10%		5%		
Damaged Egg		3%	3%		
Conspecific activity			3%		
Bonin Petrel	13%	20%			
Wedge-tailed Shearwater			5%		
Albatross spp	3%	10%			Unknown
Laysan Finch	Unknown	Unknown	NA	NA	NA
Sample Size	31	30	40	13	13

[†] Collapse caused by researcher during monitoring

*Number of lost nests is unknown

Table 2.3: Sources of known chick mortality of Tristrams' Storm-petrels breeding on Laysan and Tern Islands, Northwestern Hawaiian Islands

	Laysan 2004	Tern 2005	Tern 2006
Dead in Burrow	24%	30%	40%
Chick Missing	10%	30%	10%
Burrow Collapse	28%	10%	10%
Wedge-tailed Shearwater (direct)	28%	5%	10%
Wedge-tailed Shearwater (indirect)	7%	25%	30%
Invasive Arthropod	3%		
Number of Mortalities Observed	29	20	10

Table 2.4: Comparison of breeding success among the genus *Oceanodroma*

Species	Hatch Success	Fledge Success	Breeding Success	Source
Tristram's Storm-petrel (*O. tristrami*)	0.33	0.55	0.18	1
	0.40	0.45	0.16	2(a)
	0.57	0.49	0.28	2(b)
	0.54	<0.40	<0.22	2(c)
Band-rumped Storm-petrel (*O. castro*)	0.43	0.38	0.16	3(a)
	0.33	0.76	0.29	3(b)
Black Storm-petrel *(O. melania)*	0.53	0.91	0.48	4
Ashy Storm-petrel *(O. hymochroa)*	0.78	0.69	0.54	5
Leach's Storm-petrel (*O. leucorhoa*)	0.76	0.93	0.73	6
Fork-tailed Storm-petrel (*O. furcata*)	0.76	0.63	0.61	7
Swinhoe's Storm-petrel (*O. monorhis*)	0.51	0.80	0.41	8

1 = Marks and Leasure 1992, 2 = this study, a = Laysan Island, b = Tern Island (averaged), c = East Island, 3 = Bolton et al. 2004, a = hot season, b = cool season, 4 = Ainley and Everett 2001, 5 = Ainley 1995, 6 = Huntington et al. 1996, Kent Island, 7 = Boersma et al. 1980, 8 = inferred from Lee and Won 1988 as found in Warham 1996.

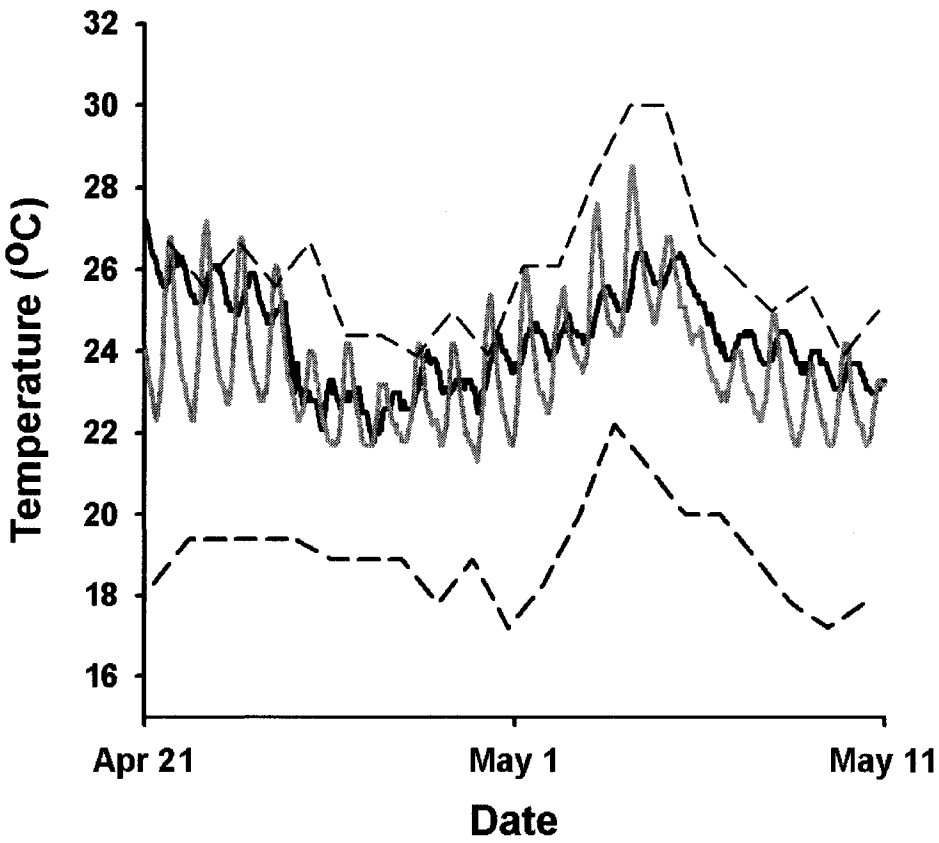

Figure 2.1: Example of earthen burrow (black) and vegetation (grey) nesting site temperatures compared to daily maximum and minimum outside ambient air temperatures (dashed), for Northwestern Hawaiian Island Tristram's Storm-petrels.

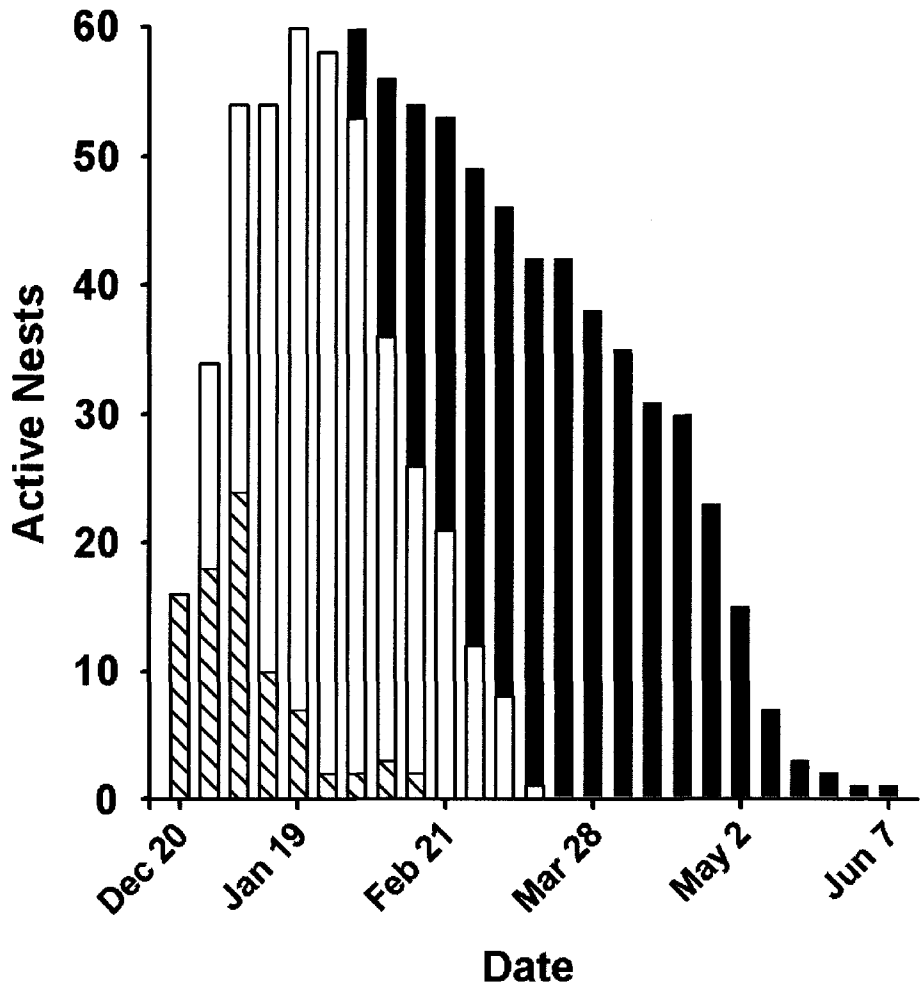

Figure 2.2: Nesting phenology of Tristram's Storm-petrel on Tern Island 2005. New nest sites are crosshatched, nest sites that continue to be incubated are white, nest sites with chicks are black.

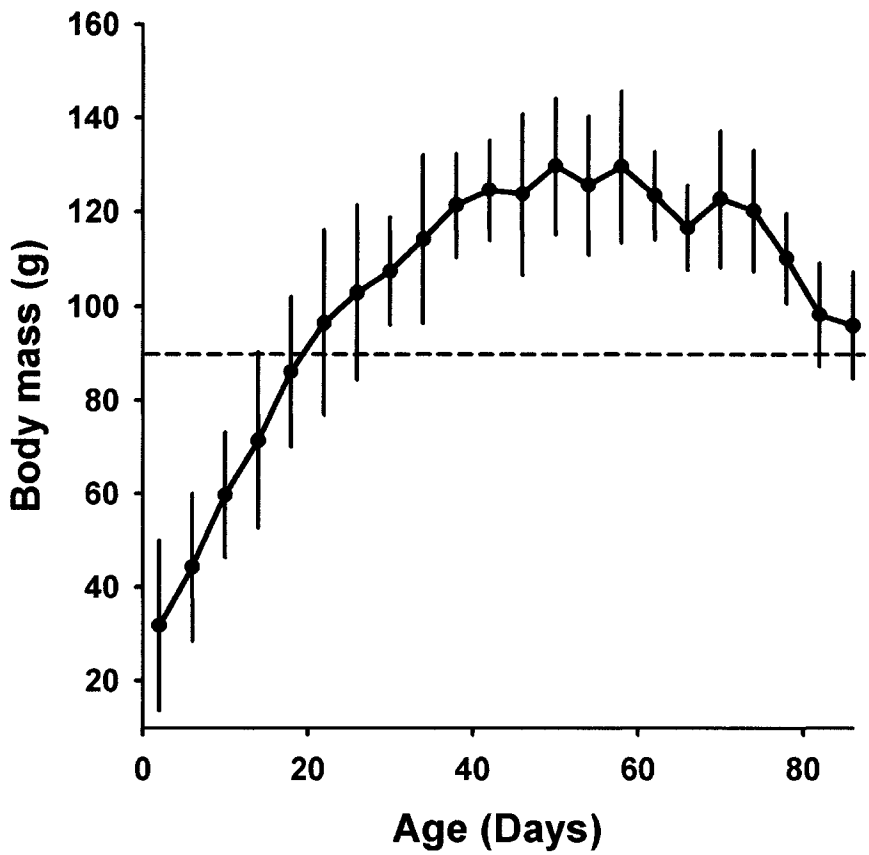

Figure 2.3: Average body mass of nestlings that survived to fledge on Tern Island 2006 (n = 12). Dashed line represents average adult mass.

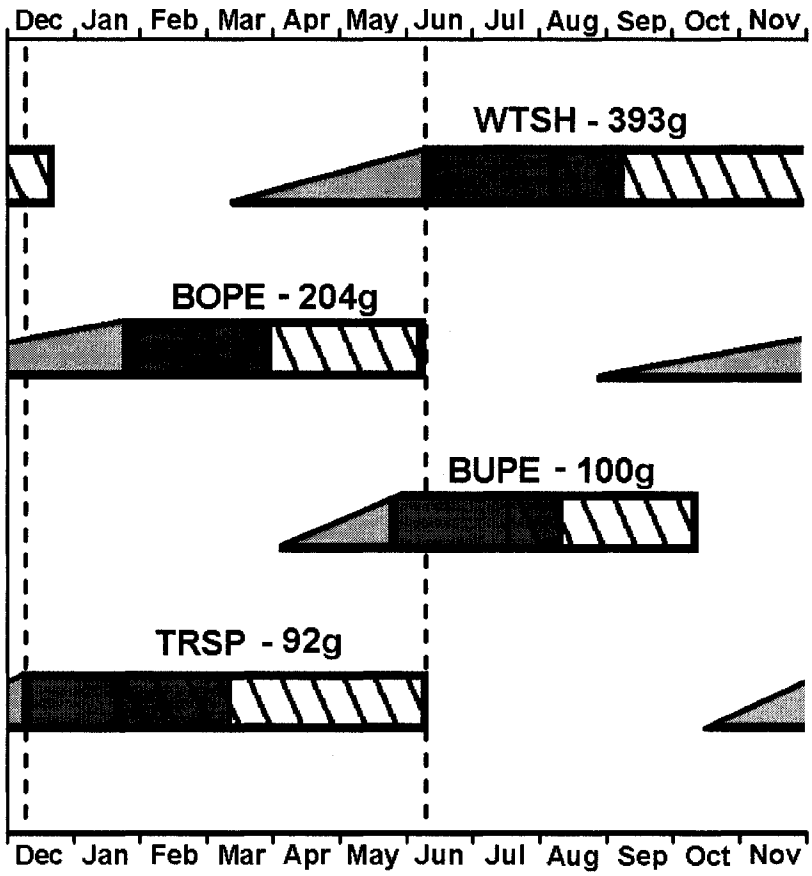

Figure 2.4: Phenology of Tristram's Storm-petrel (TRSP), Bulwer's Petrel (BUPE), Bonin Petrel (BOPE), and Wedge-tailed Shearwater (WTSH) on Tern Island 2005 (USFWS unpublished). Bonin Petrel chick data is a sample size of 1. The prospecting period is light grey, the incubation period dark grey, and the nestling period is cross-hatched.

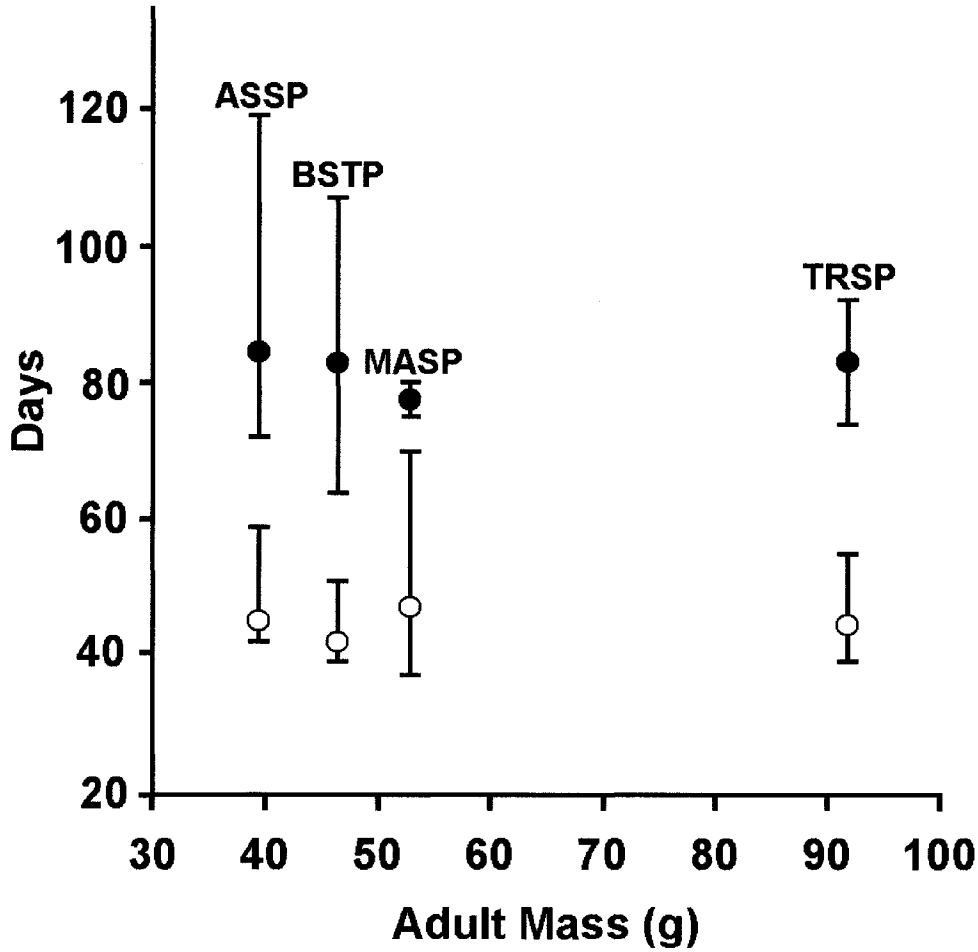

Figure 2.5: Tristram's Storm-petrel incubation (white) and fledge (black) times compared to other members of the genus breeding at similar latitudes. Data for Ashy, Band-rumped, and Markham's storm-petrels taken from Brooke 2004.

CHAPTER 3

THE INVASIVE ANT FAUNA OF LAYSAN ISLAND, HAWAIIAN ISLANDS NATIONAL WILDLIFE REFUGE (HYMENOPTERA, FORMICIDAE)

ABSTRACT

Ants are not native to any of the Hawaiian Islands and invasive ant impacts on Hawaiian ecosystems have been profound, so documentation of ant diversity is crucial to understanding and managing these alien species. Changes to the invasive ant fauna on Laysan Island, Northwestern Hawaiian Islands, were documented in 2005, fifteen years after the previous (1990) survey of the island. Six species were found on the island, all previously recorded. The common tramp ant *Monomorium pharaonis* was found to have greatly expanded its range to become the dominant ant on Laysan. During the same period, the range of the previously dominant ant species, *Tetramorium bicarinatum,* greatly decreased and the species was limited to the dense vegetation areas around the island's central lake. *Tetramorium similimum*, possibly the most recent introduction to the island, and previously the second most widespread species, was not located in surveys and is possibly extirpated. An invasive ant species has apparently not become established on Laysan in almost 20 years suggesting current quarantine measures are a successful deterrent to colonization events.

3.1 INTRODUCTION

Ants are common and often destructive invaders of ecosystems (Lubin 1984). They have the potential to negatively affect both invertebrate and vertebrate species through predation and resource competition (Le Breton 2005, Philpott et al. 2005, Gerlach 2004). In addition, invasive ants may negatively affect plant species by forming mutualistic relationships with saprophagus insects that spread fungal disease or disrupting mutualistic relationships between endemic plant species and arthropods (Ness and Bronstein 2004, Jahn et al. 2003, Bach 1991). These effects can be especially devastating on oceanic islands such as Hawaii where the native fauna has evolved in the absence of ants and lack competitive or antipredation adaptations (Paulay 1994). It is of great value to monitor the species composition and distribution of introduced ants on oceanic islands, not only as a benchmark for the global spread of introduced species, but because the species composition may shift over time (Wilson and Taylor 1967). These shifts often occur because of new introductions that change the distribution and abundance of previous invaders (Haskins and Haskins 1965). Examining such interactions may lead to better understanding the mechanisms of their success and subsequently lead to improved management and prevention of future introductions (Tsutsui and Suarez 2003). This study reports changes to the introduced ant fauna on Laysan Island, Northwestern Hawaiian Islands twenty years after the introduction of the common tramp ant *Monomorium pharaonis* (L.)

With the exception of Midway Atoll, Laysan has the highest number of invasive ant species historically documented in the Northwestern Hawaiian Islands (Nishida 2001). The spread and transportation of invasive ants was a common occurrence when

Laysan first began receiving visitation by Europeans in the mid-nineteenth century (Illingsworth 1917). Laysan's history as a guano-mining island and the ship traffic associated with it, as well as occasional visits from feather poachers, lead to the frequent introduction of invasive ants, so that four species were present by the first arthropod survey of the island in 1896 (Emery 1899). Further visitations by military personnel and scientific researchers increased the number to eight by 1962. Though this number has been cited as higher (Butler and Usinger 1963), Fullaway (1914) mistakenly identified *Monomorium destructor* (Jerdon) as *M. gracillimum* (F. Smith) (Conant and Rowland unpublished) and it is likely Butler (1961) mistakenly reported *Monomorium minimum* (Buckley) instead of *Monomorium minutum* (Mayr) in his review of the island's arthropod fauna. In addition, *Camponotus variegatus* (F. Smith) should not be included because it was collected on board a ship in close proximity to Laysan, not the island itself (Butler and Usinger 1963). The last two ant introductions were thought to have occurred in the early 1980's. *Monomorium pharaonis* was introduced circa 1984 (Conant and Rowland unpublished). The year of introduction of *Tetramorium similimum* (Mayr) is not known but sometime between 1984 and 1990 is likely (Conant and Rowland unpublished). A thorough census of the island's ant fauna had not occurred since 1990 (Conant and Rowland unpublished), leaving the current invasive ant community and their distributions poorly known.

In summary, the objective of the present study was to document the current (2005) ant species diversity and distribution of Laysan Island and compare it to the known ant community.

3.2 MATERIALS AND METHODS

3.2.1 Study area

Observations were conducted at Laysan Island (25°46 N, 171°03' W) in the Hawaiian Islands National Wildlife Refuge. Located 1495 km northwest of Honolulu, Laysan is an extremely remote 397 ha coral sand island featuring a 70 ha hypersaline lake in the centre. Once left completely void of vegetation by introduced European rabbits (*Oryctolagus cuniculus*) (see Ely and Clapp 1973), Laysan Island is currently in the midst of an island restoration project undertaken by the U.S. Fish and Wildlife Service. In 2004, approximately 217 ha, or 66% of available area, was vegetated (McClelland unpublished). The dominant vegetation is bunchgrass (*Eragrostis variabilis*), but includes dense mixed-vegetation communities (*Scaevola taccada*, *Ipomea pes-capae*, *Sicyos pachycarpus*) bordering much of the lake. Several stands of the non-native beach heliotrope (*Tournefortia argentia*) and Indian fleabane (*Pluchea indica*) are also present (see Lamoureux 1963 and Newman 1988 for more detailed vegetative community descriptions).

Laysan is the site of a year-round U.S. Fish and Wildlife Service research station and receives several visitations by ship per year. Since the establishment of the station in 1991, strict quarantine measures including the import of only new or recently frozen clothing and gear have been in place. More rigorous measures including a ban on fresh food and hull inspections for primary vessels and small boats were incorporated in 2005, following the present study (C. Rehkemper personal communication).

3.2.2 Bait Card Surveys

Wedge-tailed Shearwater (*Puffinus pacificus*) and Bonin Petrel (*Pterodroma hypoleuca*) burrows extensively undermine much of Laysan Island and travel through nesting areas poses a high risk of disturbance (Moulton and Weller 1984). Therefore the island was surveyed for ants in the early winter during a brief period when shearwater chicks had fledged and petrels had yet to start occupying burrows. A total of 182 sample locations in the island's interior were established in a 100 m grid pattern. An additional 66 locations around both the inner and outer perimeters of the vegetation were added to the survey, for a total of 248 locations (Figure 3.1). Each location was surveyed once between January 4 and 10, 2005.

For every survey location a $1cm^3$ cube of Spam© (ham, pork, sugar, salt, and water) and 1 ml each of peanut butter and honey were placed on a 4"x 6" index card. Each card was placed under a wire cage to prevent interference from shorebirds and Laysan Finches (*Telespiza catans*). The cards were left for 2-3 hours before being collected and immediately transferred to a sealed plastic bag. Because occupation of baits may be more reflective of competitive ability rather than abundance (Way et al. 1998), a relatively quick (<2 min) ground search of the immediate area was also conducted at each survey location. Collected specimens were later individually counted and identified to species following Huddleson et al. (1968).

3.2.3 Vegetation Associations

At each sample location, the 3 most abundant plant species within a 10 m radius were recorded in order of rank. Using these data, locations were later sorted into 5

vegetation types: bunchgrass, dense mixed-vegetation, bunchgrass/dense vegetation, beach heliotrope, and lake edge (*Cyperus laevigatus/Sesuvium portulacastrum*).

3.2.4 Pitfall Traps

Ant species were sampled using pitfall traps at the southern end of the lake. Traps were spaced approximately every 12m and consisted of a 266 ml plastic cup placed in a PVC tube and filled with approximately 100 ml of soapy water. Pitfall traps were active for 48 hours every 4 weeks. Sixty-eight traps were active from November 2003 to May 2004, but declined to 34 from December 2004 to March 2005. Collected specimens were later individually counted and identified to species following Huddleson et al. (1968).

3.2.4 Statistical Analysis

Correlation between ant species presence and vegetation type was tested using a binomial logistic regression model with a logit link function (Hosmer and Lemeshow 1989) in Minitab version 13 (Minitab Inc. 2000). All results were considered significant when $p \leq 0.05$. Relevant statistical models are presented in Appendix III.

3.3 RESULTS

3.3.1 Ant Species present

A total of six ant species were collected, all previously recorded on the island (Table 3.1). Ants were collected on 93% of bait cards placed in vegetated areas (n =

242). The only vegetation type in which ants were consistently absent was the lake edge association. Ants were rare in unvegetated areas and absent from outer beach areas despite high amounts of marine debris including washed-up logs. Vegetation appeared to be required for colony establishment in most locations of Laysan due to the sandy soils. Ants nested in and around the root system of plants, hollow portions of plants, or under dense vegetative cover. The highest densities of ants were consistently found under beach heliotrope, likely due to greater soil stability and the benefits associated with the high amounts of leaf litter such as increased cover and foraging opportunities.

Only 13% of locations with ants yielded more than one species ($n = 227$). The dominant ant in each location monopolized bait cards and on only 3 bait cards did the second species comprise more than 5% of collected individual ants. Ant species abundance by individuals collected and number of collection sites is presented in Figure 3.2

3.3.2 Monomorium pharaonis

Monomorium pharaonis was by far the most common ant on the island (Figure 3.3). It was found in all habitat types and dominated the bunchgrass areas where it was in most instances the only species recorded. Most bunchgrass clumps housed a nest. *Monomorium pharaonis* was also extremely common in the camp area where barriers were required to keep them out of most food items, electrical equipment, and bedding. The presence of *M. pharaonis* was strongly correlated with *Eragrostis* habitat ($G = 12.298, p \leq 0.001$, n = 248), but the species could also be found on the periphery of mixed-vegetation areas.

3.3.3 Tetramorium bicarinatum

The presence of *T. bicarinatum* was strongly correlated with the dense mixed-vegetation habitat type ($G = 27.294$, $p \leq 0.001$, $n = 248$) (Figure 3.4). Though small numbers of *T. bicarinatum* could be found foraging in bunchgrass areas, this was usually when in close proximity to mixed-vegetation and the species rarely based its colonies there.

3.3.4 Monomorium floricola

Monomorium floricola was found in both *M. pharaonis* and *T. bicarinatum* dominated areas. Though species presence could not be predicted by habitat type based on the vegetation classifications of this study, they did not occur in open bunchgrass areas and appeared to strongly prefer areas with some vegetative cover such as *S. taccada* where they were locally abundant (Figure 3.5).

3.3.5 Cardiocondyla nuda

Cardiocondyla nuda was the only species collected by bait cards that was never the dominant species on the card. Instead, the species was more often located with ground searches and may have been more widespread than indicated (Figure 3.6). Collections of *C. nuda* were most common in transition areas between bunchgrass and the thicker vegetation around the lake.

3.3.6 Plagiolepis alluaudi

Plagiolepis alluaudi may have had very limited distribution on Laysan, only being recorded in 3 isolated locations in bunchgrass habitat with an additional single specimen found dead in camp (Figure 3.7). Locally abundant, nests were noticeably larger than those of *M. pharaonis* and found in bunchgrass clumps. *Plagiolepis alluaudi* appears to have the ability to survive in areas dominated by aggressive ant species, and foraging distance may be limited (Smith 1959). Therefore, more intensive surveys for this species may have yielded more locations.

3.3.7 Hypoponera punctatissima

Hypoponera punctatissima has been described as most often locally rare with elusive habits (Delabie and Blard 2002), a trend it followed on Laysan as it was not recorded with bait cards or ground searches. Instead, all collections of this species totaled six winged females from pitfall traps. Surveys failed to locate a nest.

3.4 DISCUSSION

Though the invasive ant community on Laysan apparently changed little since the previous comprehensive survey in 1990, the distribution had changed substantially. In 1990, the most widespread ant was *T. bicarinatum*, with *M. pharaonis* restricted to only a small portion of the island near the camp area (Rowland and Conant unpublished). Since that time *M. pharaonis* had displaced *T. bicarinatum* from the bunchgrass habitat and restricted it to the dense vegetation surrounding the lake. *Monomorium pharaonis* had

been present on Laysan for twenty years but did not become the dominant species for at least seven years and possibly much longer. What factors led to this shift are unknown and require further study but Laysan demonstrates that shifts in dominance amongst invasive ants may occur gradually.

One species of ant may have been extirpated since the last survey of the island. *T. similimum*, possibly the most recently introduced species, was not recorded despite being the second most widespread species during the previous survey in 1990 (Conant and Rowland unpublished). However, it cannot be ruled out that this species was missed if it continues to persist on the island in small numbers especially considering its strong resemblance to *T. bicarinatum*.

Five of the eleven ant species recorded on the island have been extirpated in the past 110 years. However, it is possible that the extirpations of *Monomorium destructor*, *Monomorium monomorium*, and *Tapinoma melanocephalum* were greatly influenced by the ecological devastation caused by rabbits considering they were not collected after the loss of the island's vegetation (Table 3.1). Morrison (1996) found that introduced ants rarely become extirpated once introduced to Polynesian Islands. With only two extirpations since the island was revegetated, Laysan appears to support this trend. This is especially true if we consider that one of the species extirpated was *Pheidole megacephala*. This species has experienced a high level of success in both the main and Northwestern Hawaiian Islands, but was recorded in only a single survey on Laysan in 1959 and not seen again despite several additional surveys in the following years (Butler and Usinger 1963). It is possible that this record was from a very recently introduced

nonbreeding population at the time of its collection, and the species was never truly established on Laysan.

Though it was possible to rigorously document the invasive ant fauna on Laysan, their impact on the island remains relatively unexplored. Addressing this deficiency should be given the highest of priorities. Though a mass extinction of endemic arthropods likely occurred on the island due to the devastation caused by rabbits (Asquith 1995), Laysan remains an important source of arthropod biodiversity in the archipelago with at least seven endemics and numerous native species surviving (Asquith 1994). Moreover, knowledge of Laysan's native arthropod fauna is deficient taxonomically and research may yield additional endemics (Asquith 1994). The greatest threat to these remaining species is likely invasive ants, as all species of invasive ant on Laysan are insectivorous (Gray et al. 1995, Way et al. 1989, Torres 1984, Smith 1965, Sudd 1960) and are undoubtedly negative influences considering the native fauna lacks defenses against ants and other social insects. In addition, invasive ants may have indirect impacts through resource competition, facilitative relationships with other alien species, or further disruptions to Laysan's already altered ecosystem through soil excavation, seed predation, etc. (Holway et al. 2002). Having not been thoroughly surveyed for over a decade the current status of many of these species is poorly understood and additional extinctions are possible without further monitoring and research. If invasive ants are found to be negatively affecting the biota of Laysan, options into control and eradication should be explored.

Eradicating invasive ants from large natural areas is a relatively new area of research. Few eradications have been attempted and successful programs have involved

relatively small areas (<30 ha) and referred to only one or two species, ignoring other nonnative ant species that may have been present (Causton et al. 2005, Hoffman and O'Connor 2004, Abedrabbo 1994). With an area of 217 ha occupied by six ant species, eradicating ants from Laysan represents an exceptional challenge even when budgetary issues are not considered. The island's large size suggests broadcasting insecticidal bait is the only viable control method. However, broadcasting leaves the bait subject to weather effects that may limit its longevity either through reduced palatability to foraging ants or degradation of the insecticidal agent (Krushelnycky and Reimer 1998) leading to frequent reapplications. In addition, a bait or mixture of baits that is attractive to all ant species is required to prevent unaffected species from expanding their range into areas vacated by affected species. This may prove difficult considering that the widespread *M. pharaonis* may rapidly change its food preference and baits are unlikely to remain attractive over long periods of time (Edwards and Abraham 1990). In addition, some of the most commonly used ant baits such as Amdro, Maxforce, and Advance have already been found to be unattractive to *M. pharaonis* on Laysan Island (Chapter 4). Finally, the presence of endemic arthropods as well as the endemic and endangered Laysan Duck (*Anous laysanensis*) and Laysan Finch (*Telespiza cantans*) requires non-target effects to be thoroughly explored before an eradication program could be initiated and may limit options.

Though Laysan presents a number of challenges, there are a number of factors that may aid a successful eradication program. All ant species present on the island, with the exception of the uncommon *H. punctatissima,* spread by budding (Heinze et al. 2006, Trontii 2006, Astruc et al. 2001, Smallwood 1982). This suggests that if an effective

control method can be found, ant-free areas can be established, maintained, and expanded. In addition, this study found no new species of invasive ant suggesting the quarantine measures established for the island are adequate. In combination with a year-round UFWS presence to monitor for new introductions, the risk of reinvasion is low.

Perhaps the only threat to biodiversity on Laysan greater than the current invasive ant community is the introduction of additional and more aggressive ant species. Thus far Laysan has avoided the introduction of the most damaging of invasive ants including *Anoplolepis gracilipes*, *Linepithema humile, Wasmannia auropunctata, Solenopsis geminata,* and *Pheidole megacephala* (Holway et al. 2002). However, all of these species are present in Hawaii (Krushelnycky et al. 2005) with the latter two also present in the Northwestern Hawaiian Islands (Nishida and Beardsley 2002). It is imperative that quarantine measures are maintained and the island continued to be monitored for additional introductions. Without quarantine measures, the introduction of additional invasive ants to the Northwestern Hawaiian Islands is certain to occur and is a substantial threat to native fauna and flora. This is perhaps best demonstrated by Tern Island, an unquarentined island 540 km southeast of Laysan that has experienced 2 ant introductions in the past four years (Chapter 5).

Table 3.1: Invasive Ants recorded on Laysan Island, Northwestern Hawaiian Islands as of 2005

Scientific Name	Past Scientific Names*	First Reported	Last Reported	Current Status
Cardiocondyla nuda (Mayr, 1866)	N/A	1959[3]	This study	Present
Hypoponera punctatissima (Roger, 1859)	*Ponera punctatissima, P. kalakauae, P. gleadowi*	1896[1]	This study	Present
Monomorium destructor (Jerdon, 1851)	*M. gracillimum*	1896[1]	1923[3]	Extirpated
Monomorium floricola (Jerdon, 1851)	N/A	1959[3]	This study	Present
Monomorium monomorium (Buckley, 1867)	*M. minutum*	1912[2]	1912[2]	Extirpated
Monomorium pharaonis (Linnaeus, 1758)	N/A	1984[5]	This study	Present
Pheidole megacephala (Fabricius, 1793)	N/A	1959[4]	1959	Extirpated
Plagiolepis alluaudi (Emery, 1894)	N/A	1959[3]	This study	Present
Tapinoma melanocephalum (Fabricius, 1793)	N/A	1896[1]	1912[2]	Extirpated
Tetramorium bicarinatum (Nylander, 1846)	*T. guineense*	1896[1]	This study	Present
Tetramorium similimum (Mayr, 1855)	N/A	1990[5]	1990[5]	Not recorded, possibly extirpated

*refers only to past surveys of the Northwestern Hawaiian Islands

[1]Emery 1899, [2]Fullaway 1914, [3]Bryan et al.1926, [4]Butler and Usinger 1963, [5]Conant and Rowland unpublished (1990)

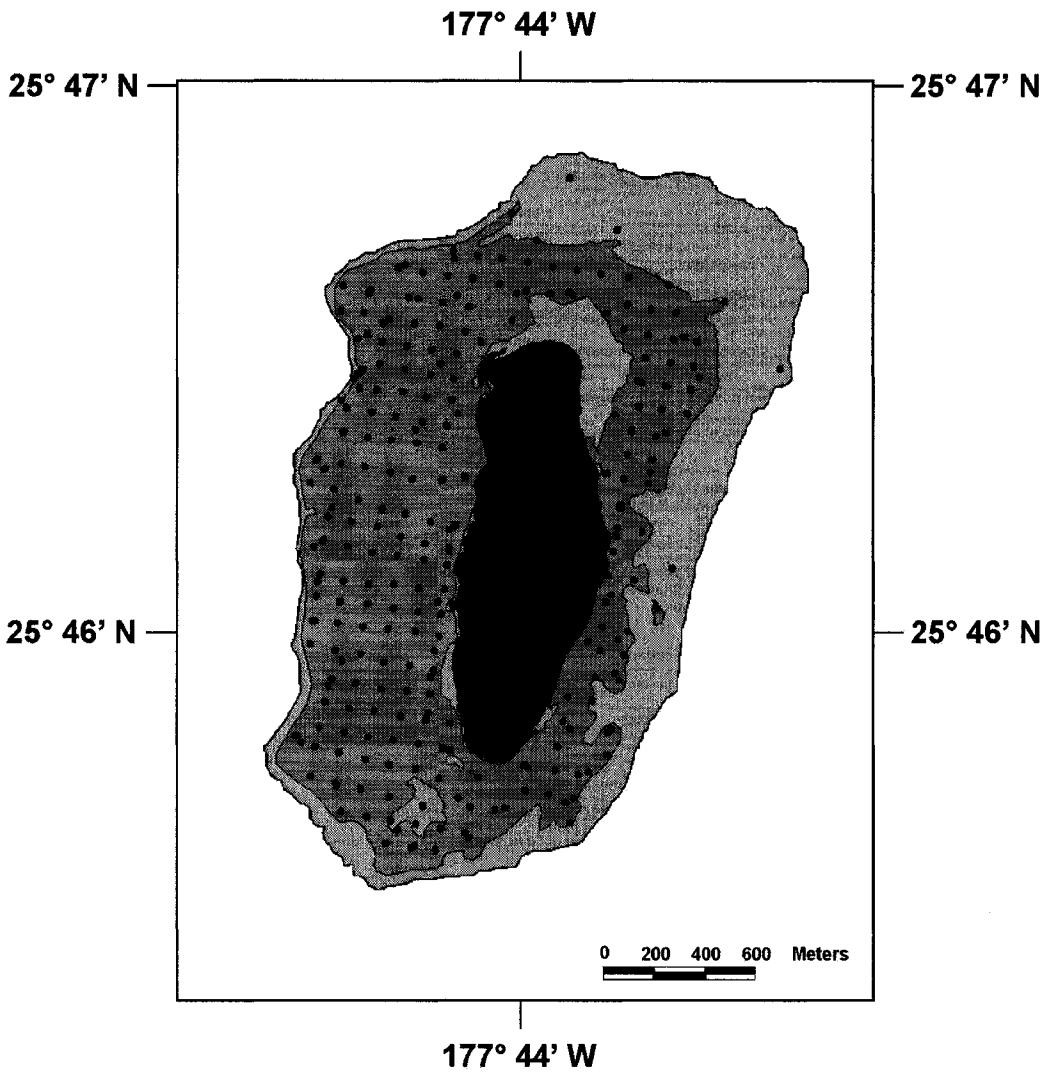

Figure 3.1: Bait card sampling locations on Laysan Island, Northwestern Hawaiian Islands. Dark grey indicates vegetated areas; black is the hypersaline lake at average winter level.

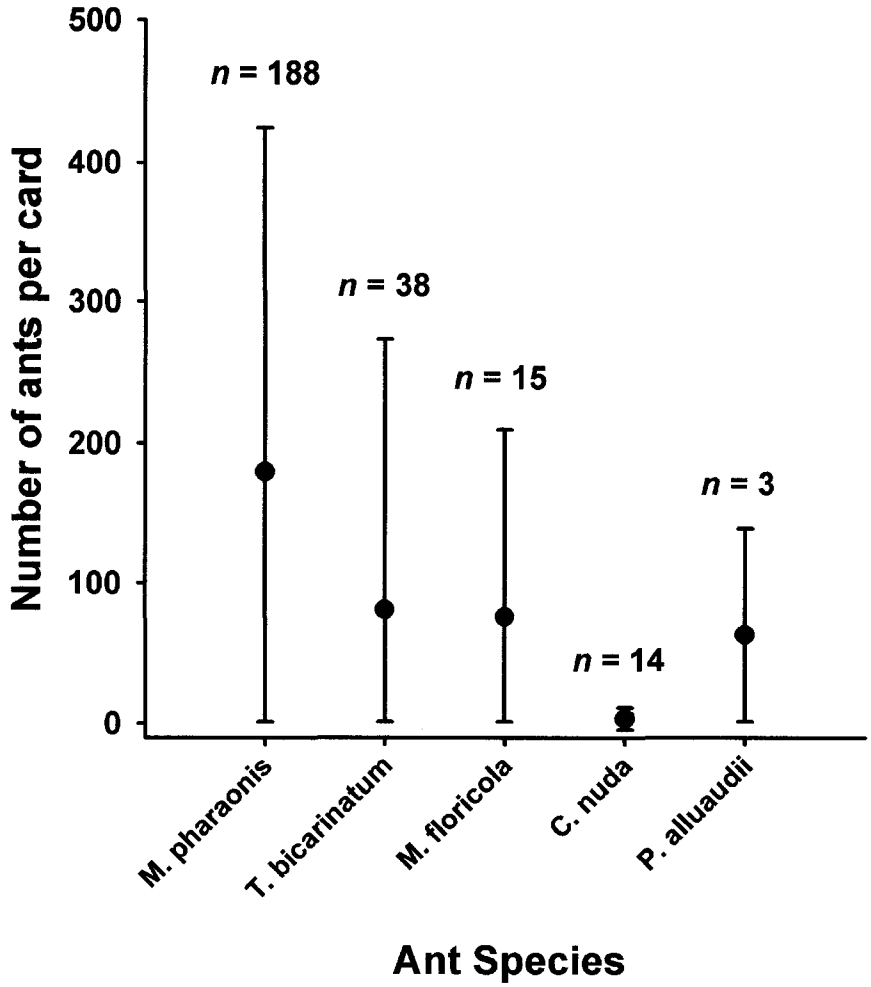

Figure 3.2: Average ant captures per baitcard on Laysan Island, Northwestern Hawaiian Islands.

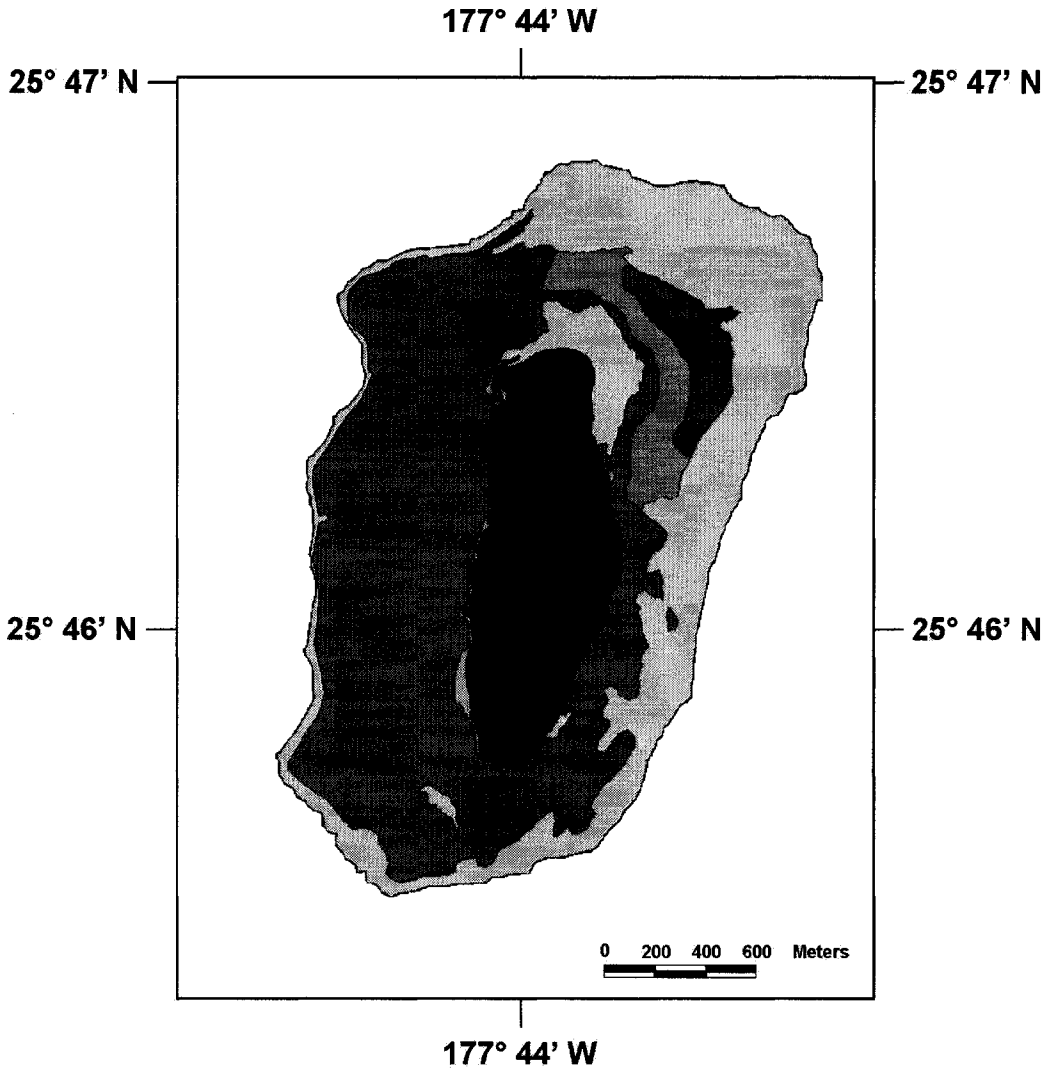

Figure 3.3: Distribution of *M. pharaonis* (darkest grey) on Laysan Island, Northwestern Hawaiian Islands. Black is the hypersaline lake, light grey is vegetation, and the lightest grey is unvegetated area.

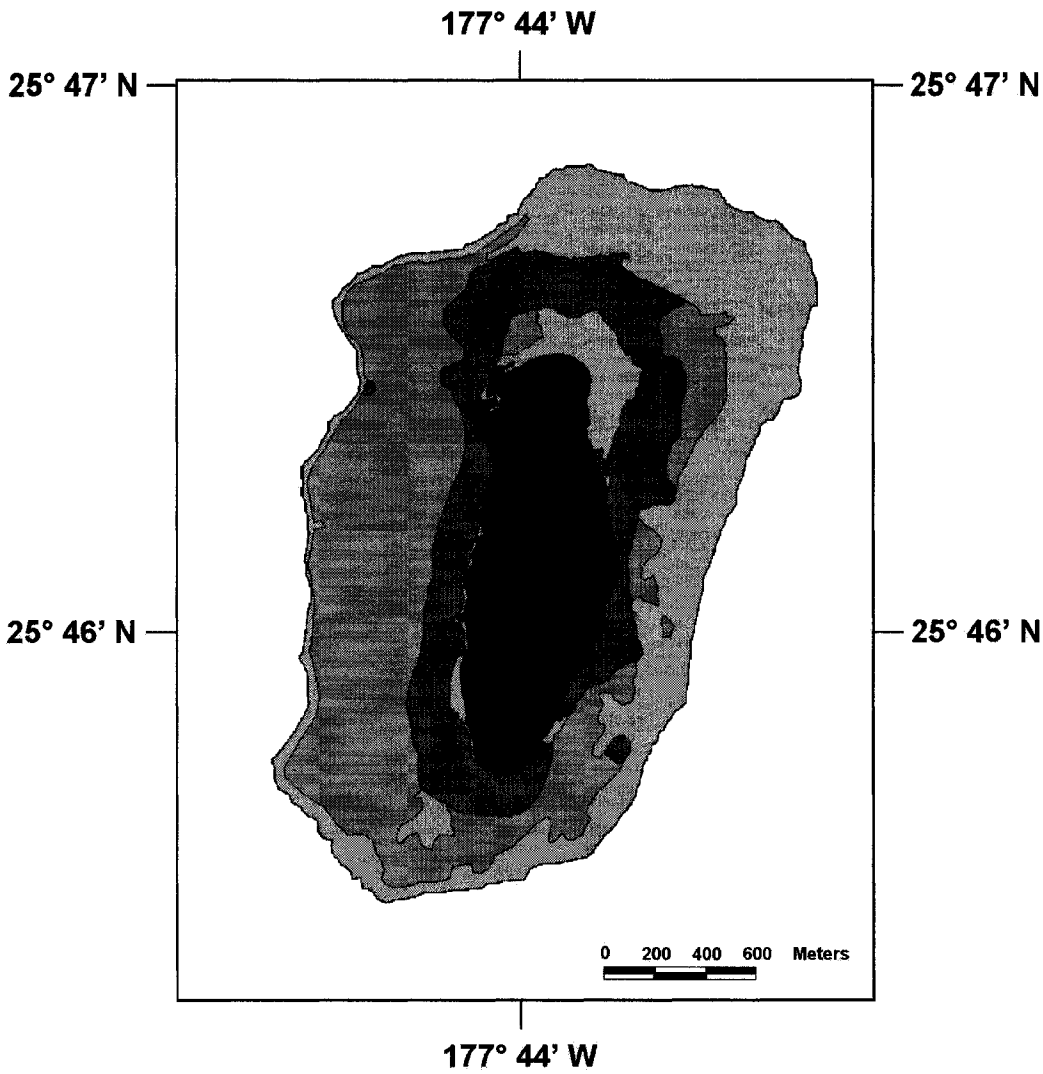

Figure 3.4: Distribution of *T. bicarinatum* (darkest grey) on Laysan Island, Northwestern Hawaiian Islands. Black is the hypersaline lake, light grey is vegetation, and the lightest grey is unvegetated area.

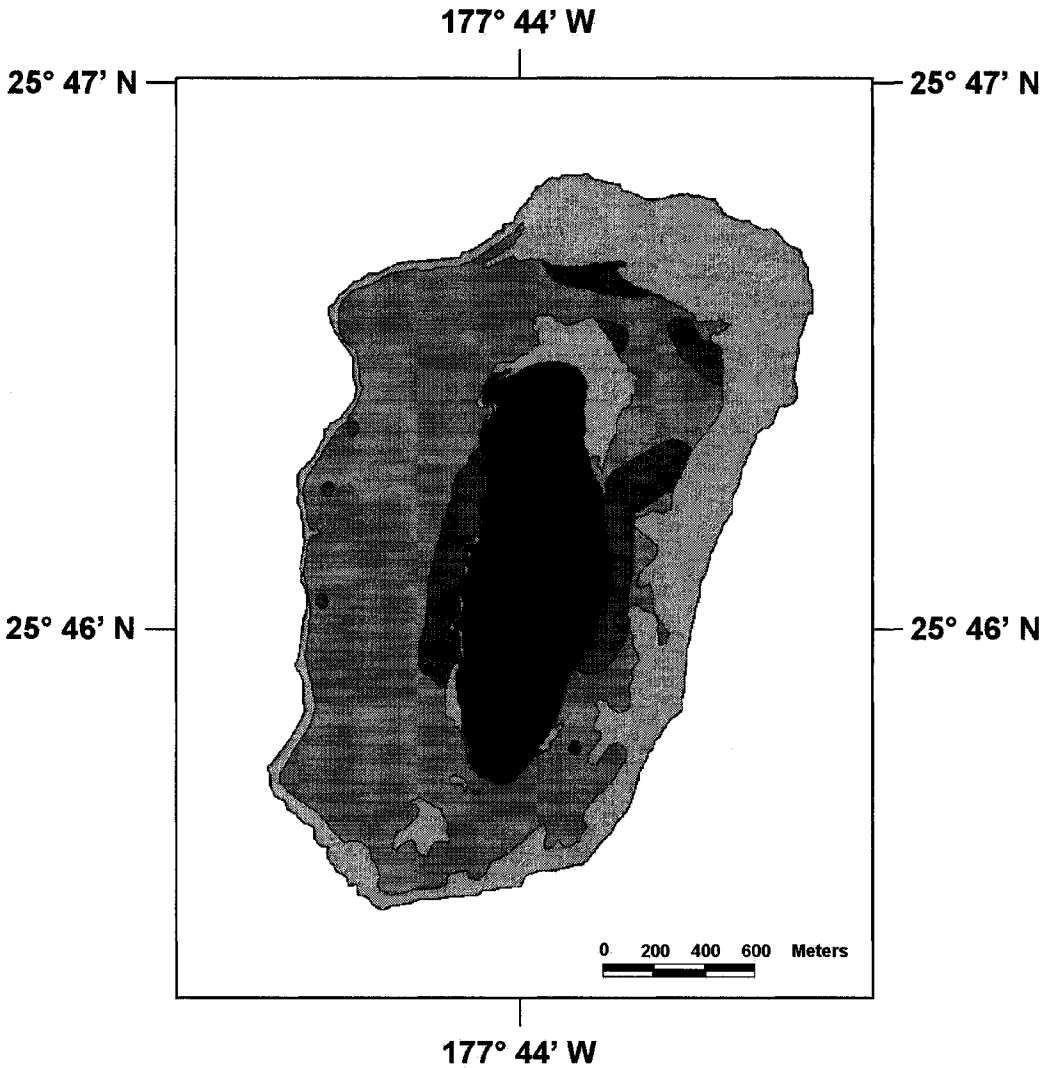

Figure 3.5: Distribution of *M. floricola* (darkest grey) on Laysan Island, Northwestern Hawaiian Islands. Black is the hypersaline lake, light grey is vegetation, and the lightest grey is unvegetated area.

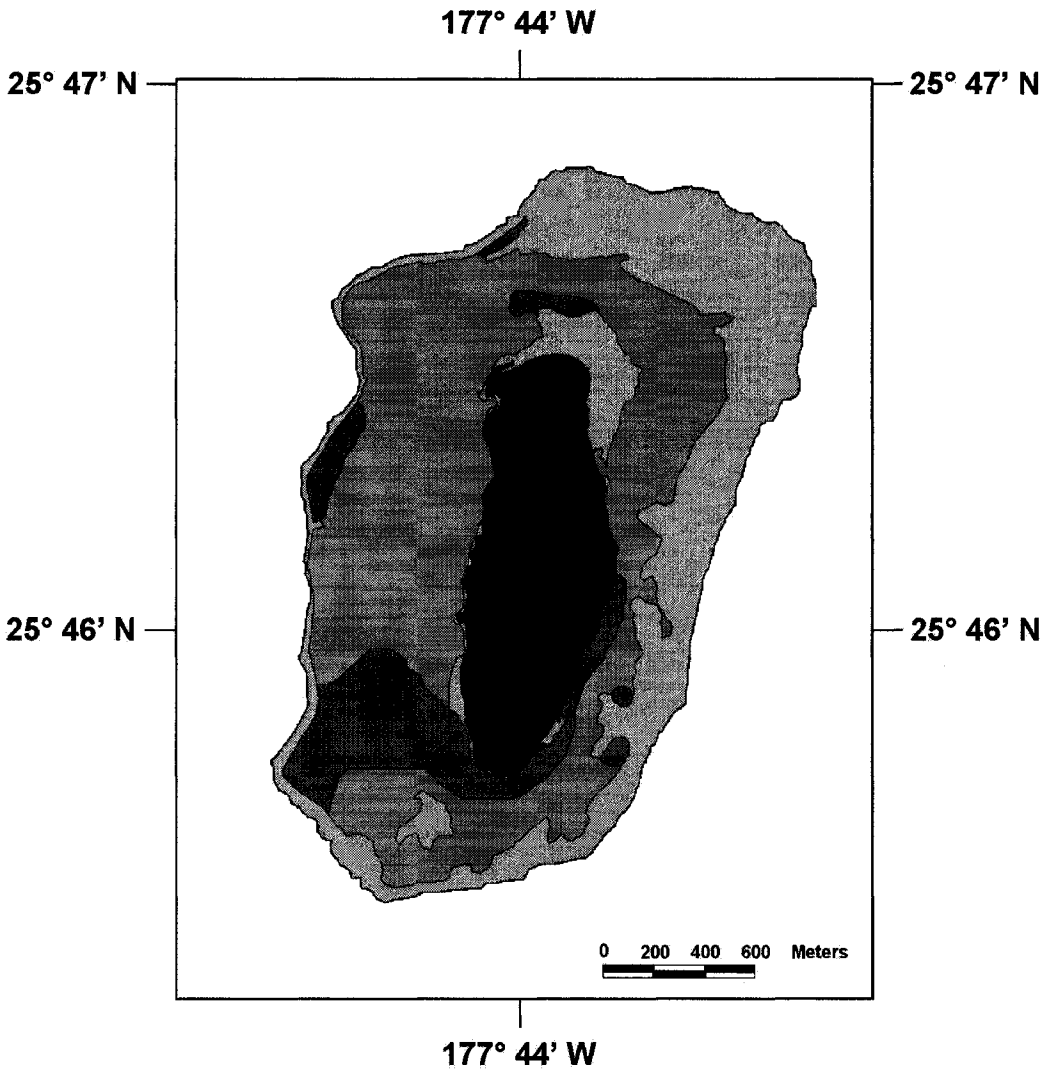

Figure 3.6: Distribution of *C. nuda* (darkest grey) on Laysan Island, Northwestern Hawaiian Islands. Black is the hypersaline lake, light grey is vegetation, and the lightest grey is unvegetated area.

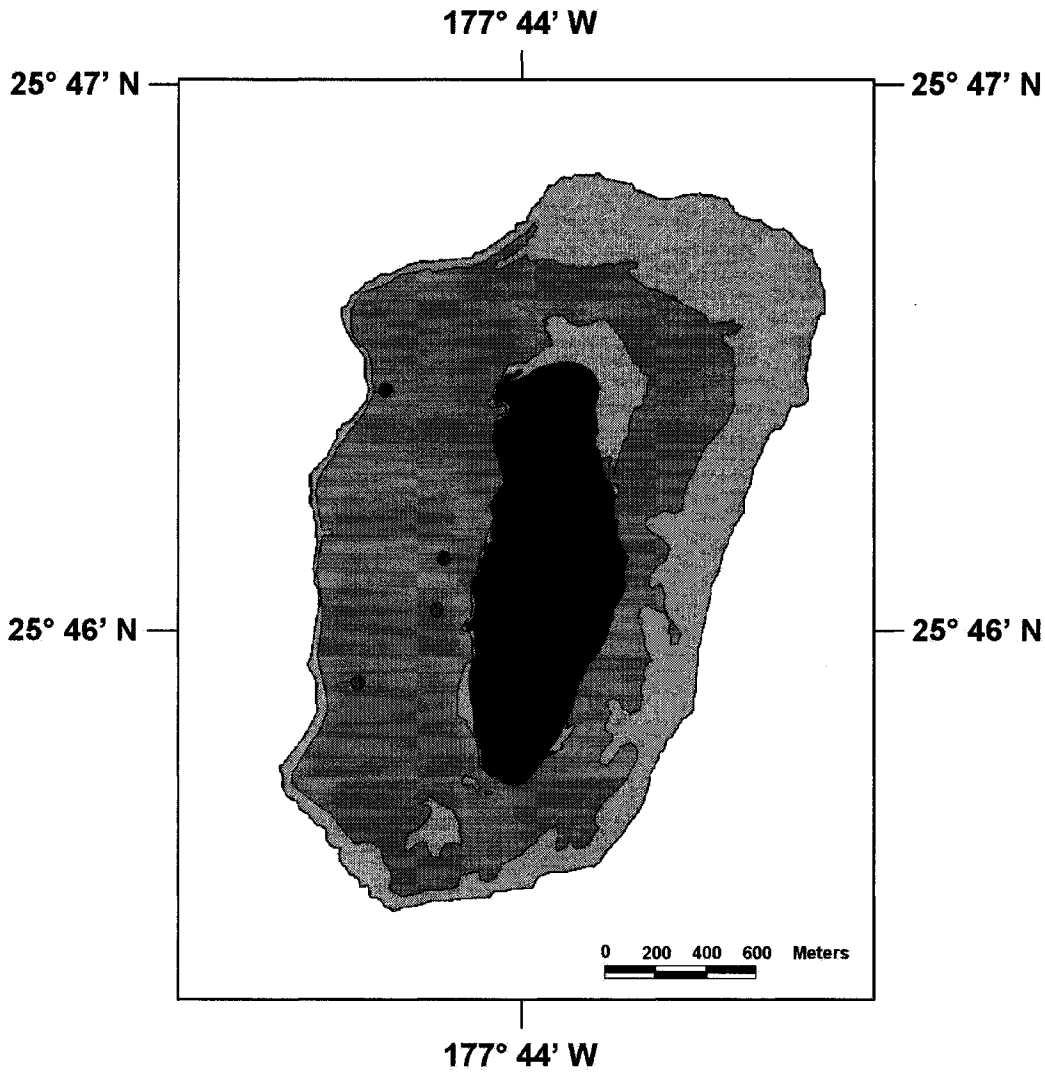

Figure 3.7: Distribution of *P. alluaudi* (darkest grey) on Laysan Island, Northwestern Hawaiian Islands. Black is the hypersaline lake, light grey is vegetation, and the lightest grey is unvegetated area.

CHAPTER 4

THE EFFECTS OF INVASIVE ANTS ON THE NESTING SUCCESS OF TRISTRAM'S STORM-PETREL, *OCEANODROMA TRISTRAMI*, ON LAYSAN ISLAND, HAWAIIAN ISLANDS NATIONAL WILDLIFE REFUGE

ABSTRACT

The possible impact of invasive ants on the avifauna of the Northwestern Hawaiian Islands was investigated by studying the breeding success of Tristram's Storm-petrel (*Oceanodroma tristrami*) on Laysan Island. This small seabird species was chosen because of its protracted winter breeding season, and its use of a wide variety of breeding habitats that would allow it to serve as an indicator for a range of other bird species. The tramp ant *Monomorium pharaonis* (L.) was found to be abundant in storm-petrel nesting areas on Laysan Island. There were 380 observations made on incubating adults and 798 observations for chicks, for a total of 1178 observations from 116 storm-petrel nest sites. No ant harassment events involving incubating adult storm-petrels were recorded. Thirteen instances of more than 5 ants on Tristram's Storm-petrel chicks were recorded. One harassment event was recorded, involving approximately 200 ants. The chick left the nest site immediately following the event, did not return, and presumably died. The number of nest failures attributed to *M. pharaonis* was 1% (n = 116). There was a significant relationship between nest type and ant interactions (G = 24.45, p = <0.0001, n

= 55), with incidents only recorded from birds nesting under vegetation. It was hypothesized that the ant interactions recorded in this study were a result of Tristram's Storm-petrel chicks being in close proximity to *M. pharaonis* nests rather than direct predation. Thus no evidence was found of a severe impact of invasive ants on the breeding success of storm-petrels at Laysan Island. Despite no direct ant impact particular attention should be given to the interactions between *M. pharaonis* and bird species reliant on vegetation for nesting cover, and studies therefore should include additional breeding bird species.

4.1 INTRODUCTION

Ants are highly successful and disruptive invaders of ecosystems (Moller 1996, Williams 1994). Their effects can be wide-ranging and extend throughout ecosystems, and may include negative population-level affects on larger vertebrates including birds. The ability of invasive ants to negatively affect birds has been documented in a number of species including Northern Bobwhite (*Colinus virginianus*) (Allen et al. 2000, Mueller et al. 1999, Giuliano et al. 1996), Sooty Tern (*Sterna fuscata*) (Feare 1999, Gerlach 2004), Least Tern (*Sterna antillarum*) (Hooper-Bui et al. 2004, Lockley 1995), Wood Duck (*Aix sponsa*) (Ridlehuber 1982), and several passerines (eg: Suarez et al. 2005, Stake and Cimprich 2003, Twedt et al. 2001) and colonial waterbirds (Drees 1994). How invasive ants impact birds is often unclear and understudied (Holway et al. 2002), but direct predation of chicks, reduced suitability of nest sites, and resource competition and displacement are confirmed or suspected (reviewed in Holway et al. 2002). Though potentially biased by the predominance of studies focusing on the red imported fire ant, *Solenopsis invicta* (Buren), ground-nesting birds with chicks confined to the nest appear to be more vulnerable and suffer higher rates of mortality than other species. In this regard, the avifauna of the Northwestern Hawaiian Islands would appear to be exceptionally susceptible to the negative effects of invasive ants. Comprising 22 native species, the avifauna of the archipelago are either ground-nesting or make use of vegetation of less than 2 m in height with chicks confined to their nests and burrows for up to several months. Finally, the birds of the archipelago lack defensive behaviour that could potentially mitigate negative effects of aggressive invasive ants having evolved in the absence of social insects.

The purpose of this study was to determine if invasive ants negatively affect the breeding success of birds at Laysan Island, Northwestern Hawaiian Islands. Laysan Island was of particular concern due to past observations that suggested invasive ants were negatively impacting the breeding success of birds, including island endemics (Conant and Rowland unpublished). These included reports of *Monomorium pharaonis* (L.) on dead Laysan Finch (*Telespiza cantans*) chicks that had been healthy the previous day, and *Tetramorium bicarinatum* (Nylander) harassing Red-tailed tropicbird (*Phaethon rubricauda*) chicks. However, both Laysan Finches and Red-tailed Tropicbirds nest at relatively low densities on Laysan (Morin and Conant 2002, U.S. Fish and Wildlife Service unpublished). To study these species would require extensive sampling effort over a large study area to achieve the needed sample size from which to draw conclusions. Therefore the investigation was focussed on Tristram's Storm-petrel.

Tristram's Storm-petrel is a species of conservation concern (U.S. Fish and Wildlife Service 2002) with several aspects of biology that make it potentially vulnerable to negative effects of invasive ants. This species is the smallest of Laysan's breeding seabirds at an average of 92 g (Marks and Leasure 1992). In addition, Tristram's Storm-petrel has one of the longest breeding seasons in the archipelago, with an average incubation length of 44 days and an average fledge length of 83 days (Chapter 2), thus both adult and chick live for long periods in habitats that possibly expose them to ant harassment. On Laysan, Tristram's Storm-petrel makes use of several nest types including earthen burrows and surface nest scrapes covered by thick vegetation (Chapter 2), which allows them to serve as potential indicators for both burrow and surface-nesting

birds. Finally, Tristram's Storm-petrel nest in colonies and thus likely could be found in relatively high densities that would be more amenable to small scale experimental manipulation.

In summary, the objectives of this study were: 1) to quantify the effects of invasive ants on the nesting success of Tristram's Storm-petrel both during incubation and the chick rearing stage; 2) to determine if the risk of negative impacts from invasive ants differs between burrow-nesting and surface-nesting birds; 3) to assess the effectiveness of three toxic ant baits for the control of alien ant populations on Laysan Island.

4.2 MATERIALS AND METHODS

4.2.1 Study area

Observations were conducted at Laysan Island (25°46 N, 171°03' W) in the Hawaiian Islands National Wildlife Refuge. Located 1495 km northwest of Honolulu, Laysan is an extremely remote 397 ha coral sand island with a 70 ha hypersaline lake in the centre. Once left completely denuded of vegetation by introduced European rabbits (*Oryctolagus cuniculus*) (Ely and Clapp 1973), Laysan is in the midst of an island restoration project undertaken by the U.S. Fish and Wildlife Service. In 2004, approximately 217 ha, or 66% of available area, was vegetated (McClelland unpublished). The re-vegetated area, however, differs from the original plant community. The dominant vegetative community is bunchgrass (*Eragrostis variabilis*), but includes dense mixed-vegetation communities (*Scaevola taccada*, *Ipomea pes-capae*, *Sicyos pachycarpus*) bordering much of the lake. Several stands of the non-native beach heliotrope (*Tournefortia argentia*) and Indian fleabane (*Pluchea indica*) are also present.

Lamoureux (1963) and Newman (1988) provided more detailed vegetative community descriptions for the island. Laysan has the highest number of invasive ant species historically documented in the Hawaiian Islands National Wildlife Refuge (Nishida 2001). Introductions likely began synonymously with human visitation starting circa 1828 (Ely and Clapp 1973) and four species had been recorded by the first arthropod survey in1896 (Emery 1899). The eleventh (but see Chapter 3) and last ant species to be recorded on Laysan was *Tetramorium similimum* (Mayr), first recorded in 1990 (Conant and Rowland unpublished). Strict quarantine procedures since then implemented by the U.S. Fish and Wildlife Service appear to have been successful in deterring additional introductions (Chapter 3).

4.2.2 Study Design

The study was conducted from November 2003 to May 2004 at the southern end of the lake in the largest of the Tristram's Storm-petrel sub-colonies. The study area was dominated by native bunchgrass with sparse low-lying plants such as *S. pachycarpus* and *Tribulus cistoides*. Two pairs of 30 x 30 m plots were established with plots separated by 50m and pairs separated by 100m (Figure 2.1). A plot in each pair was randomly selected as treatment (ant removal), with the other acting as a control. The original study design was a comparative analysis between treatment and control plots. When ant eradication efforts failed, the experiment continued as an observational study of interactions between Tristram's Storm-petrel and invasive ants.

4.2.3 Tristram's Storm-petrel Nest Site Monitoring

Storm-petrels can be negatively affected by grubbing, a traditional method of burrow monitoring where the an arm is inserted into the burrow to check for an incubating adult, egg, or chick (Blackmer et al. 2004, Boersma et al. 1980, Wilbur 1969). Tristram's Storm-petrel may be especially susceptible to disturbance from grubbing as the only previous study on this species recorded high levels of abandonment using this method (Marks and Leasure 1992). In order to keep disturbance to a minimum, all breeding sites were located and monitored in the daytime with the use of a 2.5 cm diameter infrared video probe (Peep-a-roo, Sandpiper Technologies, Inc.) briefly placed in the entrance of each burrow. In addition, at no time were adults handled or touched. Presence of an egg was inferred by the presence of an adult in incubating posture over a central nest cup at a breeding site for three consecutive nest checks over a 12-day period. Breeding sites were monitored at 4-day intervals. Adults and chicks were observed for at least 10 seconds for signs of ant harassment. If ants were observed on a chick, the chick's behaviour was documented before it was briefly removed from the nest site to better estimate the number of ants present and document possible signs of injury.

4.2.4 Ant Eradication

Laysan had not been extensively surveyed for ants since 1990 (Conant and Rowland unpublished), leaving the ant community that would be encountered relatively unknown. Due to Laysan's extreme isolation, a resupply vessel could not return to the island until 6 months after the initiation of this study. Therefore, three toxic baits that together had been documented to be effective against all species historically documented

on the island were preselected for the experiment. These were Amdro Fire Ant Bait (0.7% hydramethylnon in a corn grit matrix with soybean oil [American Cyanimid]), Maxforce Fine Granule Ant Bait (0.9% hydramethylnon in macerated silkworm pupae (*Bombyx mori*) and fish meal matrix [The Clorox Company]), and Advance 375A Select Granular Ant Bait (0.011 % abamectin B_1 in a corn grit matrix with soybean oil, meat meal, and sugar [Whitmire Micro-Gen Laboratories]). Laysan is one of only two breeding sites of the endangered Laysan Finch (*Telespiza cantans*), an extremely curious species with omnivorous habits (Morin and Conant 2002). Because Laysan Finch attraction to the poison baits was anticipated if baits were left exposed on the surface, broadcasting was not considered an option. Instead, all baits were placed in tamper-proof bait stations, enclosed in a wire cage with a wooden top to provide another barrier against finches and help protect the bait stations from the elements. Each station was provided with 5 ml of Amdro Fire Ant Bait, and 2.5 ml each of Advance and Maxforce, presented in separate compartments to track bait preference. The amount of bait consumed was estimated as either <10%, 25%, 50%, 75%, or >90% consumed by inspecting the amount of bait remaining in each compartment. Traps were spaced every 6 m for a total of 36 in each treatment plot. Baits were placed on January 6th and monitored and replaced every two weeks. Starting February 28th, changes were made to the way the granular baits were presented in an attempt to increase their attractiveness. Small amounts of honey, sugar water, peanut oil, and bacon grease were separately applied to all three baits. In addition, Maxforce, the only bait that could be easily ground, was pulverised and mixed separately with honey and sugar water. The solutions were applied to cotton batting to prevent worker ants from drowning.

4.2.5 Ant Monitoring

The substrate on Laysan is extremely sandy, and pitfall traps had to be relatively large to avoid being completely filled with blowing sand. Each pitfall trap consisted of a 7.6 cm diameter ABS tubing containing a 266 ml plastic cup. Each trap was enclosed in a wire cage constructed of 1.3 cm mesh to prevent disturbance by Laysan Finches. A total of 34 trap pairs were arranged in a cross pattern through each set of plots (Figure 2.1) and spaced every 12m, with replicates 1 meter apart. Trapping was initiated November 20 and continued every four weeks until April 14, with traps active for 48 hours.

4.2.6 Burrow Temperature

Cool burrow temperatures may protect burrowing seabirds from the negative effects of invasive ants (Krushelnycky et al. 2001). To investigate Tristram's Storm-petrel burrow temperature, Stowaway TidbiT Temp Loggers (Onset Computer Corporation) were placed in three burrows behind the nest bowl.

4.2.7 Burrow Foraging

To test the frequency of ant foraging in burrows, a sample of both occupied and unoccupied Bonin Petrel (*Pterodroma hypoleuca*) burrows were randomly selected (Tristram's Storm-petrel was considered too sensitive to disturbance). A closed plastic container measuring 9.0 x 4.0 x 1.5 cm containing 1 cm^3 of Spam© (ham, pork, sugar,

salt, and water) and 1 ml each of peanut butter and honey was inserted. Access holes were punched in eight evenly spaced locations along the sides of the box. Boxes were retrieved after two hours. For each burrow the location, entrance dimensions, if a bird was present, and if so, whether it was an adult or chick were recorded. All burrows were located in bunchgrass habitat.

4.2.9 Statistical Analysis

Results from the two control plots and the two treatment plots were each pooled. Differences in ant levels between treatment and control plots for each sampling period were analysed using a Generalized Linear Model with a Poisson error distribution and a loglink function (Hosmer and Lemeshow 1989) in the statistical program S-Plus version 7.0 (Insightful Corporation 2005), with $Pr>X^2$ values calculated separately in Minitab version 13 (Minitab Inc. 2000). Student's t distributions for 5% Type I error were also calculated in Minitab. Preliminary tests showed significant differences between treatment and control plots prior to treatment (Table 2.1), possibly due to unmeasured environmental differences e.g., bunchgrass density, food availability for ants, slope, etc. To increase confidence that treatments were the source of a change in ant population levels, the level of significance was set at above 1.5 or below 1/1.5 deviations from the intercept calculated using the link function $Y = e^u$ in Microsoft Excel 2000 (Microsoft Office, 2000). Binomial logistic regression models with a logit link function in Minitab 13 were used to analyse relationships between ant interactions and Tristram's Storm-petrel nest type, and ant visitation and Bonin Petrel burrow characteristics. Values

reported in the *RESULTS* section are means ± SD. Relevant statistical models are presented in APPENDIX III.

4.3 RESULTS

4.3.1 Nest Monitoring

There were 380 observations of incubating adults and 798 observations of chicks made over the study, for a total of 1178 observations of 116 nest sites. No instances of ant harassment of incubating Tristram's Storm-petrel adults were recorded, though on one occasion ants were found harassing an adult that had become entrapped in sand. On November 3rd, a prospecting Tristram's Storm-petrel was caught in a burrow collapse and buried to its neck, with only its head above the sand. The bird was found shortly after midnight with approximately 75 *M. pharaonis* on its head, concentrated predominately around its eyes. The bird was extracted and after its eyes were flushed with water, appeared uninjured.

Thirteen instances of more than five ants being present on Tristram's Storm-petrel chicks were recorded, constituting six of the 57 nest sites with chicks. The average number of ants on these chicks were 42.3 ± 59.2, but if the four highest counts, 52, 84, 120 (approximated), and 200 (approximated) were excluded the mean was reduced to 10.5 ± 5.4. On the chicks with the four highest counts, ants were concentrated around the chick's abdomen and cloaca, with numerous dead ants caught in the chicks down. The chick where 200 ants were observed was the only chick which appeared harassed. On that occasion the chick demonstrated foot-stomping behaviour. When checked

approximately 2 hours later, the chick was found missing from the nest site. As it was not observed again it was presumed to have died.

The number of nest failures attributed to invasive ants was 1% of all nests (n = 116), or 3% of all chick nests (n = 57). There was a significant relationship between nest type and ant interactions (G = 24.45, p = <0.0001, n = 56), with birds nesting under vegetation in surface scrapes constituting all recorded incidents.

4.3.2 Ant Species Present

Ant species recorded in the study area in order of abundance were *M. pharaonis*, *Tertramorium bicarbinatum*, *Cardiocondyla nuda* (Mayr), and *Hypopernera punctatisima* (Roger). Though it had a limited distribution and had yet to spread to the study area when last surveyed (Conant and Rowland unpublished), *M. pharaonsis* was the dominant ant in the plots, representing 99.9% of all individual ants collected. The majority of bunchgrass plants housed a nest. *C. nuda* was found throughout the study area but in low numbers. *T. bicarbinatum* was found on the periphery of the study area in association with heavier vegetative cover. *H. punctatissima* was extremely rare, with only 11 specimens collected over the course of the study.

4.3.3 Ant Eradication

Ant eradication from treatment areas was not successful, nor were the baits found to have any effect, as ant populations in the treatment plots did not differ from controls by the predetermined factor during any collection period (Table 2.1). In fact, the average

number of ants in treatment plots was higher than controls in two of the three post treatment sampling periods.

Despite frequently being found in and establishing colonies under the bait traps, *M. pharaonis* rarely if ever consumed Amdro or Maxforce, and was only occasionally witnessed taking Advance, regardless if attractants were added. At no time were foraging trails observed leading to the bait traps. The amount of bait decreased insignificantly (<10%) in the majority of traps between checks and missing bait was attributed to black larder beetles (*Dermestes ater*) that were often found dead inside the trap. Two traps placed in close proximity to dense vines in Treatment Plot B were the exception. All baits in these two traps were completely consumed in less than a week throughout the field season, though it was unknown what was consuming the bait. Both *M. pharaonis*, and *T. bicarbinatum* were found in the two unusual traps, but little foraging was observed. The number of black larder beetles in these two traps did not differ significantly from other traps in the plot. Large numbers of earwigs (*Carcinophoridae spp*) were present both in and under the two unusual traps however no dead specimens were found and their numbers did not decrease during the field season. Other traps in similar habitats elsewhere on Laysan did not experience this level of bait consumption.

4.3.5 Burrow Temperature

Average burrow temperature was 24.1° C ± 1.3 in earthen burrows with little fluctuation over a 24-hour period (AVG = 0.5° C ± 0.4, $n = 3$). The lowest recorded burrow temperature over the course of the study was 21.7° C.

4.3.6 Attraction to Burrows

Among the burrows in which bait containers were placed, 85.9% were found to contain foraging ants (n = 64), namely *M. pharaonis* (95.3 %), and *T. bicarinatum* (4.7 %). Average number of collected ants per occupied burrow was 46.1 ± 48.7 (range = 1 - 180). No significant relationship between invasive ant visitation and burrow dimension was found, nor was there a significant relationship between ant visitation and occupation by a bird.

4.4 DISCUSSION

Conclusions from this study are limited because of the failure to eradicate invasive ants from the study plots and the restriction to a single field season. However, this study did document that interactions between invasive ants and Tristram's Storm-petrel on Laysan are capable of negatively affecting Tristram's Storm-petrel breeding success. The foot stomping behaviour in the harassment event recorded in this study is similar to that described for sooty tern chicks (*Sterna fuscata*) in the Seychelles when harassed by the yellow crazy ant (*Anoplolepis gracilipes*) (F. Smith) (Robert 1999). Because it is extremely atypical for storm-petrel chicks to leave their nest site during daylight and the disappearance coincided with a strong harassment event, invasive ants were considered responsible for the chick leaving the nest site and the associated mortality. Though previously identified as a possible cause of mortality to Mississippi Kites (*Ictinia mississippiensis*; Parker 1977), the single incident here of a chick death following its harassment by 200 ants was the first confirmation of *M. pharaonis* contributing to the mortality of nestling birds. However, *M. pharaonis* did not appear

attracted to seabirds as potential prey items. The disturbance caused was primarily through aggravation as opposed to direct predation, similar to interactions between *A. gracilipes* and Sooty Terns in the Seychelles (Gerlach 2004). Though Tristram's Storm-petrel burrow temperatures were well within the tolerable range of *M. pharaonis* (Peacock et al. 1955), and ants regularly foraged in burrows, ant interactions with Tristram's Storm-petrel adults or chicks in burrows were not recorded. Nor were any chicks lost at the pipping stage when chicks are most often attacked by invasive ants (Hooper-Bui et al. 2004). Moreover, there was a significant relationship between breeding site type and presence of ants on chicks, with all observed interactions occurring at surface sites under dense vegetation. Because of the extremely sandy soil of Laysan, *M. pharaonis* was heavily reliant on the bunchgrass plants that surface-nesting Tristram's Storm-petrels used for cover, and most plants housed an ant nest in study plots. It is likely that the ant interactions recorded in this study are a result of Tristram's Storm-petrel chicks being in close proximity of *M. pharaonis* nests rather than direct predation.

Though uncommon overall, the interactions recorded between Tristram's Storm-petrel and *M. pharaonis* raise concern. This study recorded substantially higher population levels of *M. pharaonis* in the month of November compared with other months (Table 1). If *M. pharaonis* typically maintain those higher population levels in other years, there is strong potential for the level of ant disturbance on Tristram's Storm-petrel to be detrimental. The breeding success of Tristram's Storm-petrel on Laysan was relatively low and borders the level of sustainability (Chapter 2). Though by themselves these ant interactions cause few nest failures, when combined with an already low reproductive rate they may be enough to draw the colony below the level of

sustainability. Only a longer-term study would establish whether ant populations during 2003-2004 were typical, lower than average, or higher than average.

Another concern is the effect of *M. pharaonis* on other breeding bird species. If chicks in close proximity to *M. pharaonis* nests are subject to harassment events, *M. pharaonis* may decrease the breeding success of several bird species that make use of vegetative cover for nesting. These include seabirds such as the Red-tailed Tropicbird (*Phaethon rubricauda*; Shultz 2000), Christmas Shearwater (*Puffinus nativitatis*; Seto 2001), Brown Noddy (*Anous stolidus*; Chardine and Morris 1996), Sooty Tern (Feare et al. 1997) and the two endemic and endangered land birds, the Laysan Finch (Morin 1992) and Laysan Duck (*Anas laysanensis;* Moulton and Weller 1984). Laysan Finches in particular would be susceptible, as they are up to six times smaller than Tristram's Storm-petrel chicks at hatch (Morin and Conant 2002). The Laysan Duck would be less at risk to ant disturbance, as chicks leave the nest within hours after hatch (Moulton and Marshall 1996), however it is possible for ants to begin directly predating on pipping eggs or harassing adults if shifts in dietary preference occur. For example, ant colonies may shift their preference towards higher protein sources when brood is present in the colony (Sorensen et al. 1983).

Additional research is required into the effects of weather and seasonality on the population levels and dietary preferences of *M. pharaonis* and how this in turn affects the breeding success of Laysan's bird populations. Studies in the summer months when the Laysan Finch and Laysan Duck breed would be especially useful, as previous studies have shown seasonality has a large impact on the level of ant-induced chick mortality (Allen et al. 1994). In addition, broadening the study to other habitat types and ant

species is needed. For instance, in bait card surveys of the island, the non-native beach heliotrope was found to house exceptionally high populations of *M. pharaonis* compared to bunchgrass areas (Chapter 3). This was likely due to the greater soil stability, vegetative cover, and foraging opportunities. As well, the invasive ant community differs in the areas of dense vegetation around the lake area, with *T. bicarbinatum* and *Monomorium floricola* becoming more common.

The collective food preference (and thus tendency to be attracted to poison baits) of ant colonies has been found to be highly variable (Edwards and Abraham 1990) and can be influenced by a number of factors including resource availability (satiation and starvation; Loke and Lee 2006, Eow et al. 2005, Adam 2004), seasonality (Rust et al. 2000, Bristow and Yanity 1999, Hooper and Rust 1997), individual need (Cassill and Tschinkel 1999), developmental stage of the colony (Portha et al. 2002, Edwards and Abraham 1990), and bait characteristics such as formulation and particle size (Hooper-Bui et al. 2002, Hooper and Rust 1997). *Monomorium pharaonis* was listed as a target species of Advance by the manufacturer, and Maxforce had been proven effective in controlling this species in urban conditions (Oi et al 1996). However, neither was successful in controlling *M. pharaonis* on Laysan. The species was not attracted to the presented baits, nor could I improve their attractiveness by adding other attractants such as peanut oil as demonstrated in other studies (Vail et al. 1996, Vail and Williams 1994, Williams and Vail 1994).

Numerous factors could have affected bait preference, the greatest of which may have been the composition of the bait. Advance and Amdro are both oil-based baits and research has shown that carbohydrate and proteins are the best attractants of *M.*

pharaonis (Chong et al. 2002). In addition, the baits suffered from poor longevity in Laysan's humid climate and likely contributed to the lack of appeal. Maxforce began caking and showing signs of mould in less than a week, as it has in other environments in Hawaii (Krushelnycky and Reimer 1998). Amdro and Advance were much more resistant to caking, but mould would begin to appear at the end of 2 weeks. Bait particle size may also have been a factor as *M. pharaonis* has been demonstrated to prefer bait sizes between 420 and 590 μm, while Maxforce and Amdro have particles of 1000 to 2000 μm (Hooper-Bui et al. 2002).

Another possible reason for the lack of bait acceptance on Laysan was an overabundance of alternative food items. Carrion is extremely common on Laysan year round due to the high populations and diversity of seabirds found on the island (see Fefer et al 1984). The amount of carrion likely reaches peak levels in winter due to large numbers of dead albatross chicks. These seabird carcasses are also abundant sources of sarcophagus insects and their larvae. Such copious resources could play a large role in bait acceptance.

Though numerous studies into the control of *M. pharaonis* have been conducted, unfortunately most have occurred in laboratory or temperate urban environments (e.g.: Buczkowski et al. 2005, Eow et al. 2005, Lim and Lee 2005, etc.). The current study on Laysan demonstrated the difficulty of controlling *M. pharaonis* in a natural setting and the need for further research under conditions where numerous environmental factors may affect bait acceptance.

Table 4.1. Changes in pitfall trap captures between treatment and control plots before and following eradication efforts on Laysan Island, Northwestern Hawaiian Islands.

	AVG/Trap ± SD		$Pr>X^2$	t value	Deviation
	Treatment	Control			
Nov 25	297.9 ± 197.9	306.0 ± 195.0	0.020	-2.32	0.85
Dec 24	169.9 ± 198.5	175.0 ± 160.5	0.123	-1.54	1.04
Jan 21	232.9 ± 237.4	214.9 ± 200.0	<0.001	5.04	0.90
Treatment	.....				
Feb 18	63.9 ± 61.8	47.5 ± 48.4	<0.001	9.54	0.88
Mar 24	203.4 ± 174.7	207.0 ± 196.0	0.323	-0.99	1.06
Apr 14	216.2 ± 224.5	174.3 ± 161.4	<0.001	12.59	0.96

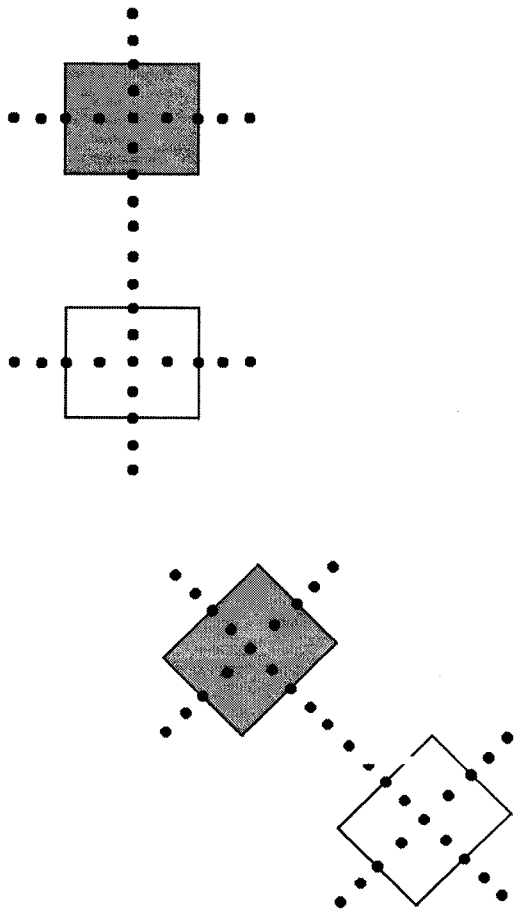

Figure 4.1. Arrangement of pitfall trap pairs between treatment (grey) and control plots (white) on Laysan Island, Northwestern Hawaiian Islands.

CHAPTER 5

THE EFFECTS OF THE BIGHEADED ANT, *PHEIDOLE MEGACEPHALA (F.)* ON THE FLEDGING SUCCESS OF TRISTRAM'S STORM-PETREL, *OCEANODROMA TRISTRAMI*, ON TERN ISLAND, HAWAIIAN ISLANDS NATIONAL WILDLIFE REFUGE

ABSTRACT

An investigation was carried out on the effects of the bigheaded ant, *Pheidole megacephala* (F.), on the fledging success of Tristram's Storm-petrel (*Oceanodroma tristrami*) on Tern Island, Hawaiian Islands National Wildlife Refuge during 2004-2005. The research compared a treatment plot, in which ants had been eradicated, and a control plot. No significant difference the fledging success of Tristram's Storm-petrel between plots was found ($G = 3.98$, df = 1, $p = 0.046$).but higher fledging success was recorded in the control plot, where the bigheaded ants remained. Control of *P. megacephala* was achieved in treatment plot by using a ratio of 1.5:1 Maxforce Granular Ant Bait to Advance 375A Select Granular Ant Bait broadcasted at a rate of 2.3 kg/ha. Bait traps, containing the same ratio of bait, spaced every 6 m along the perimeter, successfully prevented reinfestation. It was concluded from this work that eradicating *P. megacephala* from Tern Island is feasible. A total of six ant species were found, one a new record and another an apparent reintroduction and points to the lack of quarantine procedures that are needed to prevent further introductions.

5.1 INTRODUCTION

Ants are among the most destructive of invasive species, capable of widespread ecosystem change and biodiversity loss (Porter and Savignano 1990). Their effects can be especially devastating on oceanic islands that have evolved in the absence of social insects (Reimer 1994). There is perhaps no better example than the effects of the invasive Bigheaded Ant, *Pheidole megacephala* (F.), on the lowland ecosystems of the main Hawaiian Islands. The species is abundant in habitats below 600 m and has been responsible for the elimination of numerous populations of native insects (Zimmerman 1970). The success of *P. megacephala* is aided by its ability to achieve extremely high densities and its aggressive nature (Gillespie and Reimer 1993). The invaded range of *P. megacephala* is not limited to the main Hawaiian Islands, but has spread to include several of the Northwestern Hawaiian Islands as well (Nishida 2001). Comprising nine islands, atolls, and shoals, these much older and smaller islands show little resemblance to the main islands in many respects such as climate, elevation, rainfall, etc. However, like the main islands, the endemic fauna of Northwestern Hawaiian Islands evolved in absence of social insects. As a result, *P. megacephala*, if established, can be expected to be equally disruptive to Northwestern Hawaiian island ecosystems, perhaps more so given their small size.

Concerns have been raised that *P. megacephala* has a negative impact on nesting seabirds in the Northwestern Hawaiian Islands. The ability of invasive ants to negatively affect the breeding success of birds has been documented in a number of species (Holway et al. 2002) and the seabirds of the archipelago may be vulnerable. Comprised of 19 native species, Northwestern Hawaiian Islands seabirds predominately nest on or near the

ground and have chicks confined to the nest site for several months. Among the species of concern is Tristram's Storm-petrel (*Oceanodroma tristrami*). Several aspects of Tristram's Storm-petrel biology appear to make it especially vulnerable to invasive ants. The species is the smallest ground-nesting seabird in the archipelago at an average of 92 g (Marks and Leasure 1992). In addition, Tristram's Storm-petrel has one of the longest breeding seasons, with an average incubation length of 44 days and an average fledge length of 83 days (Chapter 2), subjecting both adult and chick to long periods of exposure to ant harassment. A study was initiated to investigate the impact of this ant in response to recent observations on Tern Island, French Frigate Shoals that indicated *P. megacephala* as a contributing factor in the death of Tristram's Storm-petrel chicks (McClelland and Jones personal observation).

The objectives of the study were: 1) Quantify the effects of invasive ants at Tern Island on the nesting success of Tristram's Storm-petrel 2) Assess the efficacy of two toxic ant baits in controlling *P. megacephala* populations on Tern Island, and 3) Document the invasive ant fauna of Tern Island.

5.2 MATERIALS AND METHODS

5.2.1 Study area

Tern Island (23° 52' N, 166° 17' W) is one of several coral sand islets at French Frigate Shoals, a crescent-shaped coral atoll located 955 km northwest of Honolulu. Measuring 13.8 ha (U.S. Fish and Wildlife Service 2002), Tern is the site of a U.S. Fish and Wildlife Service Research station and one of only two islands in the shoals that currently support both vegetation and appreciable seabird populations. The island lacks

strict quarantine protocols and receives visitation by a supply plane on a monthly basis. Supplies and building materials including lumber are landed at a wharf on the southwest side of the island. Invasive ants were recorded on the island as early as 1914 (Swezey 1915). By the time of this study seven invasive ant species had been recorded including *P. megacephala,* first collected in 1984 (W.C. Gagne, unpublished). At the time of this study, *P. megacephala* was the dominant ant species in all outside areas and in and near all man-made structures (Richardson 2000).

The Tristram's Storm-petrel colony on Tern Island was limited to a single 0.1 ha area on the southern side of the island dominated by the non-natives beach heliotrope (*Tournefortia argentea*) and nettleleaf goosefoot (*Chenopodium murale*).

5.2.2 Study Design

Investigations were conducted from December 2004 to June 2005. Two 30 x 30 m plots were established separated by an 18 m buffer area encompassing the Tristram's Storm-petrel colony. Plots were arbitrarily selected as treatment (ant removal) and control plots. Tristram's Storm-petrel colony size in terms of both area and population was poorly understood prior to the study. There was no prior information on storm-petrel breeding success in different parts of the colony, so to the study could not employ a study design such as a BACI (Before-after controlled impact) design (Stewart-Oaten et al. 1986). The assumption of the study was that a difference in storm-petrel productivity between treatment and control plots would reflect the impact of ants on productivity. In order to ensure the study plots encompassed a sufficient number of birds, the establishment of treatment and control plots, and therefore ant eradication, was delayed

until after the majority of storm-petrels had initiated breeding. As a result, the focus of this study was on the effects of invasive ants on the fledging success of Tristram's Storm-petrel chicks and did not directly address issues such as adult harassment, distribution of nest sites, etc.

5.2.3 Tristram's Storm-petrel Nest Site Monitoring

Storm-petrels can be negatively affected by grubbing, a traditional method of burrow monitoring where the an arm is inserted into the burrow to check for an incubating adult, egg, or chick (Blackmer et al. 2004, Boersma et al. 1980, Wilbur 1969). Tristram's Storm-petrel may be especially susceptible to disturbance from grubbing as the only previous study on this species recorded high levels of abandonment using this method (Marks and Leasure 1992). In order to keep disturbance to a minimum, all breeding sites were located and monitored in the daytime with the use of a 2.5 cm diameter infrared video probe (Peep-a-roo, Sandpiper Technologies, Inc.) briefly placed in the entrance of each burrow. In addition, at no time were adults handled or touched. Presence of an egg was inferred by the presence of an adult in incubating posture over a central nest cup at a breeding site for three consecutive nest checks over a 12-day period. Breeding sites were monitored at 4-day intervals. Adults and chicks were observed for at least 10 seconds for signs of ant harassment.

5.2.4 Ant Eradication

Two baits were selected based on the results of their effectiveness against *P. megacephala* in the Northwestern Hawaiian Islands (Reimer unpublished): Maxforce Granular Ant Bait (1.0% hydramethylnon [The Clorox Company]), and Advance 375A Select Granular Ant Bait (0.011 % abamectin B_1 [Whitmire Micro-Gen Laboratories]). The two baits were mixed at a ratio of 1.5:1 Maxforce to Advance and broadcasted at a rate of 2.3 kg/ha. A single broadcast application was made on February 3rd in concert with the placement of bait stations. Each bait station contained 2.5 ml of the same bait mix, placed 6 m apart around the perimeter of the treatment plot. Baits in stations were monitored and replaced every 2 weeks.

5.2.5 Ant Monitoring

Ants were monitored with both pitfall traps and bait cards. Pitfall traps were similar to that described by Majer (1978) and consisted of two 2.5 cm diameter glass test tubes resting in a sleeve of rubber tubing (Figure 5.1) that was capped with a cork stopper when not in use. A 30 cm metal plate separated each tube. A total of 19 traps were spaced every 6 m through the 2 study plots, starting and ending 18 m beyond the borders of the control and treatment plots. Sampling was conducted every 2 weeks from December 28 to May 26. Traps were active for 24 hours per day.

Bait cards were placed in a variety of habitats including the several buildings on the island for a census of the island's ant fauna. Each card consisted of a 1 cm^3 of Spam©

(ham, pork, sugar, salt, and water) and 1 ml each of peanut butter and honey placed on a 7.6 x 12.7 cm index card. Cards were placed every 75 m in vegetated areas of the island, in all buildings, and additional areas that may have contained additional ants species such as the few coconut palms on the island. Each card was placed under a wire cage to prevent interference from scavenging birds. Cards were collected after 1 hour and it and all ants present were transferred immediately to a plastic bag. Sampling occurred from April 1 to April 7.

5.2.7 Tick Monitoring

Ant presence may benefit birds by suppressing avian tick populations by preying on nymphs and eggs (Duffy 1991). To account for this possibility, the avian tick *Ornithodoros capensis* was collected in pitfall traps coinciding with ant monitoring.

5.2.8 Statistical Analysis

Differences between treatment and control plots for both ant and avian tick populations for each sampling period were analysed using a Generalized Linear Model with a Poisson error distribution and a loglink function (Hosmer and Lemeshow 1989) in the statistical program S-Plus version 7.0 (Insightful Corporation 2005), with $Pr>X^2$ values calculated separately in Minitab. Student's *t* distributions for 5% Type I error were also calculated in Minitab. Pretreatment pit fall trap data showed a significant difference in ant populations between treatment and control plots (Table 5.1). To be confident that treatments were the source of any changes in ant population levels, the

level of significance was set at above 1.5 or below 1/1.5 deviations from the intercept calculated using the link function $Y = e^{u}$ in Microsoft Excel 2000 (Microsoft Office 2000).

A binomial logistic regression model with a logit link function was used in Minitab version 13 (Minitab Inc. 2000) to compare fledge success between control and treatment plots. Timing of breeding between plots was analyzed with a general linear model in Minitab after hatch dates had been categorized as weeks into the breeding season. All results were considered significant when $p \leq 0.05$.

Values reported in the RESULTS section are means ± SD. Relevant statistical models are presented in APPENDIX III.

5.3 RESULTS

5.3.1 Fledging Success

A significant difference in fledge success was found between treatment and control plots when controlled for known sources of mortality ($G = 3.98$, $p = 0.046$, $n = 12$). However, it was the control plot that experienced the higher fledging success (Control = 0.89, Treatment = 0.50, $n = 17, 12$ respectively). No interactions between *P. megacephala* and Tristram's Storm-petrel were recorded in 469 observations of incubating adults, or 486 observations of chicks of various age. No eggs were lost at the pipping stage.

5.3.2 Ant Species Present

Pheidole megacephala was the dominant ant in the study plots prior to control efforts, representing 99.9% of all captures. *Cardiocondyla nuda* (Mayr) was found near the study area in limited numbers. Several winged specimens of *Hypoponera punctactissima* (Roger) were also collected. Additional species of ant collected but confined to buildings well outside the study area were *Paratrechina longicornis* (Latreille), *Ochetellus glaber* (Mayr), and *Tapinoma melanocephalum* (F.). Though *P. longicornis* had been previously recorded on Tern Island (Beardsley 1966), the species was likely a recent reintroduction considering it was not recorded by Richardson (2000). This was the first record of *O. glaber* from Tern Island and from anywhere in the entire Northwestern Hawaiian Islands. Two previously recorded species, *Tetramorium bicarinatum* and *Monomorium floricola* (Richards 2000), were not recorded.

5.3.3 Ant Eradication

Pheidole megacephala was successfully controlled in the treatment plot and differed by the set level of significance in all months following treatment (Table 5.1). *Pheidole megacephala* population levels dropped significantly within 2 weeks of application on the treatment plot (Figure 5.1), though *C. nuda* continued to persist at low levels throughout the study, as it had prior to treatment. The bait traps were effective in preventing reinfestation of the treatment area. Though foraging *P. megacephala* could still be found on occasion along the plot border, we assume these were foraging scouts from colonies outside of the plot. *Pheidole megacephala* was found in high densities 6 m outside of the treatment area, suggesting colonies have a very limited foraging area.

5.3.4 Tick Populations

Average avian tick captures per pitfall trap were similar between treatment and control plots before bait application (4.1 ± 3.0, $n = 40$ and 4.3 ± 2.4, $n = 104$ respectively). Avian tick captures increased in both the treatment and control areas following treatment (4.7 ± 3.1, $n = 50$ and 4.6 ± 2.7, $n = 126$ respectively) and captures did not differ significantly between the two plots over the remainder of the study ($Pr>X^2 = 0.65$, $t = - 0.45$, $n = 126$).

5.4 DISCUSION

The study found no evidence that *P. megacephala* negatively affected the fledging success of Tristram's Storm-petrel chicks during the 2005 breeding season. In addition to chick survival being higher in control areas, no incidences of chick harassment were recorded over the course of the study. Why chick survival was higher in the control area (ants present and abundant) than in the treatment area (ants reduced to very low numbers) was unknown. One possible explanation is the quality of the Tristram's Storm-petrel parents. There was a significant difference between the hatch dates in the treatment and control plots ($F = 8.77$, $p = 0.01$, $n = 35$), with chicks hatching in the control plot an average of two weeks earlier. A general tendency related to timing of breeding amongst birds is that breeding pairs of higher quality will breed earlier than those of lower quality (Lack 1968). Higher quality pairs require less time to forage prior to the onset of the breeding season and are the first to choose their mates. This allows them to choose

breeding sites of the highest quality. Soil type is a significant factor in the location of storm-petrel colonies (Stenhouse and Montevecchi 2000, Harris 1974) and Tristram's Storm-petrel appears to strongly adhere to this trend (Chapter 2). Presumably this tendency follows down to individual burrow selection and the highest quality breeders are concentrated where soil type is most favourable. The soil in the control plot was noticeably less sandy and burrow density was higher with 24% more burrows ($n = 58$) than the treatment plot. It is hypothesized that these differences in soil quality lead to a higher percentage of high quality breeders nesting in the control plot, which ultimately lead to a significantly higher fledge success.

Other possibilities that could explain the results were that some aspect of the treatment (ant poison) might have reduced breeding success in the treatment area, or that the birds in the control area benefited from the higher ant population present. Neither of the poisons used are very toxic to birds (Vander Meer et al. 1982, Fisher and Mrozik 1992) and the birds were not directly or indirectly exposed to the poison at their nest sites, eliminating treatment artefacts as an explanation Avian tick populations did not differ significantly between the control and treatment plots and no other possible benefit of ant presence is known. In retrospect, only a BACI or similar experimental design could have provided a clear test of ant effects in this situation, but as the study was for one season this was not possible.

The results of this study differ from observations reported from other islands in the archipelago that also contain populations of *P. megacephala*. At Kure Atoll seabird chicks were often found with holes bitten in their feet in areas in which *P. megacephala* densities were high (Krushelnycky et al. 2005). Reports suggested that the densities of *P.*

megacephala on Kure were much higher than they were on Tern (E. Flint personal communication). This is likely due to the presence of introduced *Verbesina encilioides* that supports high densities of alien scale insects. *Pheidole megacephala* forms mutualistic relationships with scale insects, allowing both to increase in number (Bach 1991). Though scale insects were present on Tern (Nishida 2001), in particular on the alien nettleleaf goosefoot (McClelland, personal observation), it was likely that plant densities were not high enough on Tern to support such high populations of scale insects and *P. megacephala* as on Kure.

Another factor relevant to population levels of *P. megacephala* recorded on Tern in 2005 may have been precipitation. Rainfall has been found to negatively affect population levels of *P. megacephala* (Beardsley et al. 1982) and the Northwestern Hawaiian Islands typically experience increased rainfall in the winter months. December 2004 received an exceptionally high rainfall of 180 mm (Figure 5.2). It is possible this high rain event negatively affected the *P. megacephala* population on Tern Island prior to when pitfall trap collections began on January 4. Further research into the population levels of *P. megacephala*, both in drier winters and in typically drier seasons such as summer, are required.

The relative ease of eradication of *P. megacephala* from the treatment area suggested that eradicating this species from the island would be economically feasible both in material and labour costs, at least during the winter season. Though *P. megacephala* was not found to negatively affect Tristram's Storm-petrel, it was without a doubt a negative influence on the island's native arthropod fauna. The ability of this species to negatively impact Hawaiian arthropod fauna has been well documented

(Gillespie and Reimer 1993, Zimmerman 1970, Perkins 1913). Though a wide-scale inventory of the arthropod fauna of Tern Island was beyond the scope of this study, past surveys suggest indigenous and endemic arthropods are rare (Nishida 2001). In addition, this species may further alter the ecosystem as it may negatively affect native Hawaiian plants (Howarth 1985) and benefit aliens (Bach 1991). The eradication of *P. megacephala*, as well as the other invasive ant species, from Tern Island should be strongly encouraged. However, a note of caution is required. Tern Island is an unquarantined island that receives regular visitation. As a result, two species of invasive ant (*Paratrechina longicornis* and *Ochetellus glaber*) have become established in the last 4 years. Without addressing the underlying cause of these species' invasions of the island, Tern Island will continue to be invaded by invasive ants.

Table 5.1: Differences in ant population levels between control and treatment plots before and after eradication efforts on Tern Island, Northwestern Hawaiian Islands.

	AVG/Trap ± SD				
	Treatment	Control	Pr >ChiSq	t value	Deviation
Jan 4	18.4 ± 12.5 $n = 10$	31.0 ± 31.7 $n = 26$	0.06	-1.88	0.91
Jan 25	18.1 ± 27.2 $n = 10$	17.8 ± 21.1 $n = 26$	<0.001	4.63	1.33
Feb 8	2.5 ± 1.7 $n = 10$	10.0 ± 12.3 $n = 26$	0.021	-2.26	0.75
Feb 22	3.2 ± 6.0 $n = 10$	11.4 ± 17.7 $n = 26$	0.008	-2.61	0.75
Treatment	.....				
Mar 3	1.4 ± 1.0 $n = 10$	15.0 ± 13.5 $n = 26$	<0.001	-6.58	0.30
Mar 18	0.6 ± 0.8 $n = 9$	41.7 ± 75.9 $n = 26$	<0.001	-3.99	0.13
Apr 1	3.1 ± 1.7 $n = 10$	56.8 ± 69.5 $n = 25$	<0.001	-13.43	0.25
Apr 15	0.6 ± 1.1 $n = 10$	43.6 ± 88.1 $n = 24$	<0.001	-4.55	0.10
Apr 29	1.7 ± 2.6 $n = 10$	38.0 ± 73.7 $n = 26$	<0.001	-6.78	0.18
May 13	2.0 ± 2.6 $n = 10$	42.1 ± 60.3 $n = 25$	<0.001	-6.58	0.19

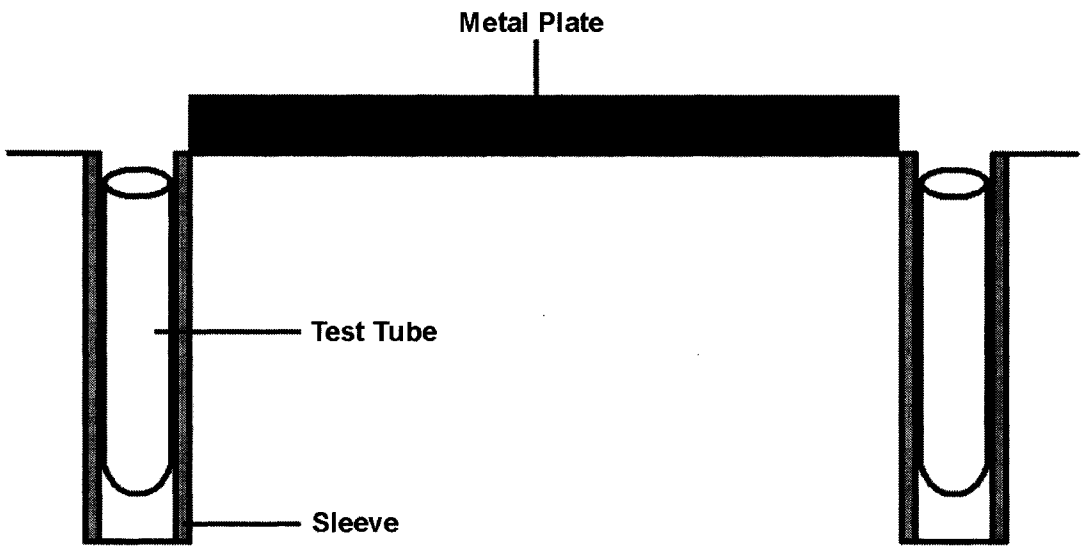

Figure 5.1: Pitfall trap design used on Tern Island, Northwestern Hawaiian Islands, 2005.

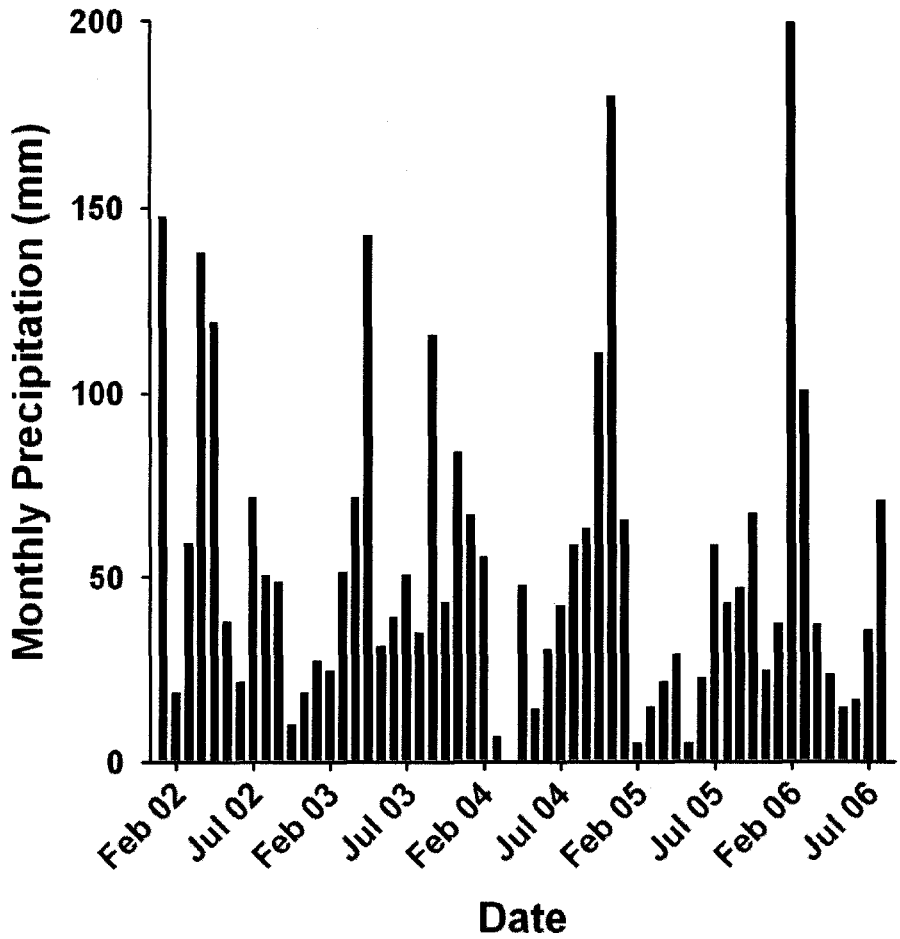

Figure 5.2: Monthly precipitation (mm) on Tern Island from January 2002 to August 2006.

CHAPTER 6

SUMMARY

To investigate the effects of invasive ants on Tristram's Storm-petrel (*Oceanodroma tristrami*) in the Northwestern Hawaiian Islands this study has asked and answered three questions.

Question 1: What is the basic breeding biology and population size of Tristram's Storm-petrel on Laysan Island and French Frigate Shoals?

This study was the most comprehensive analysis of Tristram's Storm-petrel breeding biology to date and greatly improves our knowledge of this poorly known species. Tristram's Storm-petrel was found to have a relatively low reproductive rate on Laysan (0.16), Tern (0.28), and East (<0.22) islands. Nest abandonment was the greatest cause of nest failure in all years and locations, however, no relation was found between abandonment and frequency of nest site visitation. The next most important factors impacting breeding success were nest site competition with larger burrowing seabirds and weather effects.

The population estimate of 700 Tristram's Storm-petrel breeding pairs on Laysan Island is lower but comparable to past estimates (Rauzon et al. 1985, Ely and Clapp 1973). This study was the first to estimate the Tristram's Storm-petrel population at French Frigate Shoals. It was estimated that 252 - 280 Tristram's Storm-petrel pairs breed on Tern and East islands, with a potential third colony on La Perouse Pinnacle. Though our knowledge of this species is improved, many questions remain unexplored.

Future research should focus on Tristram's Storm-petrel demography and age of first breeding. Efforts should be made to quantify the breeding populations on other islands and studies occurring on non-sand islands are also required. Finally, knowledge of Tristram's Storm-petrel diet and at sea distribution would greatly improve our ability to conserve and protect this species.

Question 2: What are the current invasive ant communities of Laysan Island and French Frigate Shoals and is eradication feasible?

This study documented the current invasive ant fauna on Laysan and Tern islands. Species communities had changed greatly on both islands since the mot recent surveys. On Laysan, *Tetramorium similimum* had possibly been extirpated while the common tramp ant *Monomorium pharaonis* was found to have greatly expanded its range. During the same period the range of the previously dominant ant species, *Tetramorium bicarinatum,* greatly decreased.

Pheidole megacephala was found to dominate Tern Island both in and out of doors. Two species, *T. bicarinatum* and *Monomorium floricola* were not recorded and were possibly extirpated. Two species, *Paratrechina longicornis* and *Ochetellus glaber*, had both been introduced in the past four years reflecting Tern Island's lack of quarantine protocols.

Laysan and Tern islands represent two contrasting problems in terms of eradication. Eradicating invasive ants from Laysan is a daunting task due to the island's size. In addition, discovering a control method that is both effective against all species present and has acceptable non-target effects may prove difficult. However, a new

species of ant has not been recorded on Laysan in twenty years suggesting quarantine protocols are adequate. If the difficulties of eradicating ants can be overcome, it is possible that a successful eradication would be permanent.

Tern Island is in direct contrast to Laysan. This study demonstrated that eradicating *P. megacephala* from a small area on Tern Island was possible and the small size of the island suggests that expanding treatments may successfully eradicate the species. In addition, the dominance of *P. megacephala* has limited the distributions of most other ant species suggesting most other species of invasive ant may also be eradicated. However, the introduction of new ant species to the island is relatively common and Tern Island will continue to be invaded by ants unless the lack of quarantine protocols is addressed.

Question 3: Do invasive ants negatively affect the breeding success of Tristram's Storm-petrel in the Northwestern Hawaiian Islands?

The failure to successfully control *M. pharaonis* on Laysan Island and the limitation of a single field season severely limit conclusions on the effects of invasive ants on Tristram's Storm-petrel on Laysan Island. However, this study did document that *M. pharaonis* is capable of causing chick mortality through interactions resulting from Tristram's Storm-petrel chicks being in close proximity of *M. pharaonis* nests. Though the interactions between *M. pharaonis* and Tristram's Storm-petrel were not predatory, the potential for similar interactions with other surface-nesting species is cause for concern. Additional research is required into the effects of weather and seasonality on the population levels and dietary preferences of *M. pharaonis* and how this in turn affects

the breeding success of Laysan's bird populations. In addition, broadening the study to other habitat types and ant species is needed.

The study found no evidence that *P. megacephala* negatively affected the fledging success of Tristram's Storm-petrel chicks during the 2005 breeding season. In addition to chick survival being higher in control areas, no incidences of chick harassment were recorded over the course of the study. *Pheidole megacephala* populations on Tern Island may have been suppressed by high rainfall prior to the study. Further research into the population levels of *P. megacephala*, both in drier winters and in typically drier seasons such as summer, are required.

This study was the first to investigate the effects of invasive ants on a ground-nesting bird in the Northwestern Hawaiian Islands as well as the first to comprehensively study the breeding biology of Tristram's Storm-petrel and quantify the species' population at two breeding sights. In regard to the latter, this study has greatly improved our understanding of this poorly studied species' biology. However, the main objective of this study, to quantify the effects of invasive ants, has not achieved the same success. The inability to control *M. pharaonis* on Laysan Island and the restriction of a single field season severely limited the conclusions from this study. Though the ability of invasive ants to cause mortalities to birds on Laysan Island was documented, the full impact of their presence on Tristram's Storm-petrel and other ground-nesting birds remains unanswered. The study on Tern Island also suffered from the restriction of a single field season. Though *P. megacephala* was found to have no affect on Tristram's Storm-petrels,

it is possible populations were suppressed and populations of *P. megacephala* are higher under different environmental conditions.

The recurring conclusion from this study is the need for additional research. As such, this study should be regarded as a preliminary assessment of the effects on invasive ants on Tristram's Storm-petrel and other ground-nesting birds in the Northwestern Hawaiian Islands. Future research should focus on the effects of weather and seasonality on invasive ant population levels and how this affects ground-nesting birds. Efforts should also be made to regularly monitor invasive ant communities and record new introductions. Finally, regardless if invasive ants negatively affect bird populations, they are undoubtedly a negative influence on the native arthropods in the archipelago. To preserve biodiversity in the archipelago, future research must include quantifying interactions between invasive ants and endemic arthropods.

Appendix I: Summary of Tristram's Storm-petrel Research and Observations in the Northwestern Hawaiian Islands

Nihoa Island

1964 – First recorded observation of Tristram's Storm-petrel breeding on Nihoa. Two dead chicks collected (Clapp et. al 1977).

1965 – Population estimated at 150 birds (maximum). One adult banded, a second collected as a specimen (Clapp et. al 1977).

1969 – Two adults banded (Clapp et. al 1977).

1981 – Population estimated at 2 000 – 3 000 breeding pairs (Rauzon et al. 1985).

– Two stomach samples collected for diet analysis (Harrison et al. 1983).

1978 to 1983 – Adult measurements taken and several birds collected as specimens (Rauzon et al. 1985).

Necker Island

1965 – One adult found dead (Clapp et al. 1977).

1979 – First recorded observation of Tristram's Storm-petrel breeding on Necker (one chick) (Rauzon et al. 1985).

1982 - One mummified chick collected (Rauzon et al. 1985).

French Frigate Shoals

1891 - "a few pairs" observed on East Island sitting on the sand and 2 specimens collected (Rothchild 1893-1900). Note - The birds are described as sitting under vegetation in the early morning. This is atypical behaviour for Tristram's Storm-petrel and leads to speculation the birds collected were actually Christmas Shearwaters (*Puffinus nativitatis*), another black though considerably larger procellarid for which such behaviour is common.

1966 - First recorded observation of Tristram's Storm-petrel breeding on Whale-Skate Island (2 adults and 1 dead chick) (Amerson 1971).

1967 – Population count of 6 birds on Whale-Skate Island (Amerson 1971).

1969 – One mummified adult found on La Perouse Pinnacle (Amerson 1971).

- Population count of 6 birds on Whale-Skate Island (Amerson 1971).
- One adult observed outside of the USCG barracks on Tern Island (Amerson 1971).

1985 – Population of Whale-Skate and East islands estimated at 10 to 15 breeding pairs based on personal observations by Eilerts (Rauzon et al. 1985).

1993 - First recorded observation of Tristram's Storm-petrel breeding on Tern Island (USFWS unpublished).

1995 - Annual population surveys and chick banding commence on Tern Island, recording on average 19 breeding pairs each year with a peak of 32 in 2002 (USFWS unpublished). Note - the methodology used in surveys has been shown to have a large potential for error (McClelland unpublished).

Laysan Island

1896 – Specimens collected (Rothchild, 1893-1900).

1902 – Population described as "hardly common" (Fisher 1903)

1912 - Population described as "not common" (Dill and Bryan 1912)

1912 – High breeding failure due to heavy rains followed by a sand storm. Population estimated at 20 000 breeding pairs (Willet 1919).

1965 – Population estimated at 2 000 – 3 000 breeding pairs (Ely and Clapp 1973).

1966 – Population estimated at 1 500 breeding pairs at the beginning of the breeding season (Ely and Clapp 1973).

1978 to 1983 – Adult measurements taken and several birds collected as specimens (Rauzon et al. 1985).

1979 to 1981 – Eight stomach samples collected for diet analysis (Harrison et al. 1983).

1980 to 1983 – Fourteen stomach samples collected for pollution analysis (Boersma 1986).

1985 – Population estimated at 500 – 2 500 breeding pairs (Rauzon et al. 1985).

1986 to 1987 – 35 stomach samples (18 adults, 17 chicks) collected for marine debris analysis (Sileo et al. 1990).

1992 - Marks and Leasure (1992) publish first study of Tristram's Storm-petrel breeding biology. Measurements on a large number of breeding adults are collected

Lisianski Island

1979 to 1981 - Mummified Tristram's Storm-petrel remains collected (Rauzon et al. 1985).

1981 - No Tristram's Storm-petrels found during a Bonin Petrel survey (Rauzon et al. 1985).

Pearl and Hermes Reef

1979 – No significant numbers of young found in mid-May (Rauzon et al. 1985)

1984 – Population estimated at 1 000 – 2 000 breeding pairs (Fefer et al. 1984)

1985 – Population estimated at 300 – 500 breeding pairs (Rauzon et al. 1985 based on Amerson et al. 1974).

2002 – Population estimated at 1 343 breeding pairs (Wegmann and Kropidlowski 2002).

Midway Atoll

1979 to 1983 – No evidence of Tristram's Storm-petrel observed despite frequent visits (Rauzon et al. 1985).

1981 – Adult male with enlarged testes found dead on Sand Island (Grant 1982).

1997 – First breeding attempt at Midway Atoll recorded on Sand Island (Baker et al. 1997).

Kure Atoll

1963 to 1966 – 27 adults banded, no recoveries (Woodward 1972).

1964 – One adult collected as a specimen (Woodward 1972).

1969 – Two adults banded (Woodward 1972).

1972 – "probably a rare breeder…no eggs or nestlings found" (Woodward 1972).

The Northwestern Hawaiian Islands Archipelago

1984 – Population estimated at a total of 21 740 birds (7 500 breeding pairs, 6 740 nonbreeders) (Fefer et al. 1984).

1990 – Population "probably numbers no more than 10 000 birds" (Harrison 1990).

Appendix II: The ant fauna of Tern Island, French Frigate Shoals, 2005.

Scientific Name	First Recorded	Distribution	Behaviour
Cardiocondyla nuda (Mayr)	1923[1] (unspecified island within FFS)	Out of Doors	Less abundant than most tramp ants. Capable of existing with more aggressive ant species[5]
Hypoponera punctatissima (Roger)	1923[1] (unspecified island within FFS)	Out of Doors	Locally rare with elusive habits. Not a dominant species[6]
Pheidole Megacephala (Fabricius)	1984[2]	Island-wide	Aggressive and abundant. A dominant species capable of displacing other ant species[7]
Tapinoma melanocephalum (Fabricius)	1990[2]	Indoors	Unaggressive colonizer of buildings and urban environments able to compete with more aggressive ant species by rapid recruitment to food sources[8]
Ochetellus glaber (Mayr)	2005[4]	Indoors	Arboreal species with very few details of its biology known
Paratrechina longicornis (Latreille)	1962[3], 2005[4] following initial extirpation	Restricted to the boathouse and tractor shed	Aggressive species capable of dominating habitats but can be displaced by more aggressive ant species such as *P. megacephala*[9]

[1]Bryan et al. 1926, [2]Conant and Rowland unpublished, [3]Beardsley 1966, [4]this study, [5]Heinze et al. 2006, [6]Delabie and Blard 2002, [7]Gillespie and Reimer 1993, [8]Clark et al. 1982, [9]Banks and William 1989.

Appendix III: Statistical Models

CHAPTER 2

Model 1: Relationship between hatch success and nest site characteristics

Success ~ Nest Type + Location + Burrow Length + Burrow Curve + Burrow Entrance Size, family = binomial (link = logit)

'Success' = hatched egg or failed egg

'Nest Type' = earthen burrow, vegetated nest scrape, or rock crevice

'Location' = study area 1, 2, 3, 4, 5, or 6

'Burrow Length' = burrow length (cm)

'Burrow Curve' = burrow curved or was straight

'Burrow Entrance Size' = burrow entrance size (cm^2)

Model 2: Relationship between fledge success and nest site characteristics

Success ~ Nest Type + Location + Burrow Length + Burrow Curve + Burrow Entrance Size, family = binomial (link = logit)

'Success' = fledged chick or failed chick

'Nest Type' = earthen burrow, vegetated nest scrape, or rock crevice

'Location' = study area 1, 2, 3, 4, 5, or 6

'Burrow Length' = burrow length (cm)

'Burrow Curve' = burrow curved or was straight

'Burrow Entrance Size' = burrow entrance size (cm^2)

Model 3: Relationship between hatch success and lay date

Success ~ Lay Date, family = binomial (link = logit)

'Success' = hatched egg or failed egg

'Lay Date' = week into the breeding season

Model 4: Relationship between fledge success and lay date

Success ~ Lay Date, family = binomial (link = logit)

'Success' = fledged chick or failed chick

'Lay Date' = week into the breeding season

Model 5: Relationship between nest abandonment and monitoring frequency (controlled for other known sources of failure)

Abandonment ~ Monitoring Frequency, family = binomial (link = logit)

'Abandonment' = egg hatched or abandoned

'Monitoring Frequency' = nest sites checked every 4, 7, or 21 days

Model 6: Relationship between nest abandonment and breeding season on Laysan Island (controlled for other known sources of failure)

Abandonment ~ Breeding Season, family = binomial (link = logit)

'Abandonment' = egg hatched or abandoned

'Breeding Season' = 2004 or 2005

Model 7: Relationship between nest abandonment and island at French Frigate Shoals (controlled for other known sources of failure)

Abandonment ~ Island, family = binomial (link = logit)

'Abandonment' = egg hatched or abandoned

'Island' = Tern Island or East Island

Model 8: Relationship between nest abandonment and minor collapses at the burrow entrance (controlled for other known sources of failure)

Abandonment ~ Collapse, family = binomial (link = logit)

'Abandonment' = egg hatched or abandoned

'Collapse' = burrow did or did not suffer a minor collapse at the burrow entrance

Model 9: Relationship between Bonin Petrel Annexation and nest site characteristics

Annexation ~ Nest Type + Location + Burrow Length + Burrow Curve + Burrow Entrance Size, family = binomial (link = logit)

'Annexation' = nest site annexed or not annexed by a Bonin Petrel

'Nest Type' = earthen burrow, vegetated nest scrape, or rock crevice

'Location' = study area 1, 2, 3, 4, 5, or 6

'Burrow Length' = burrow length (cm)

'Burrow Curve' = burrow curved or was straight

'Burrow Entrance Size' = burrow entrance size (cm^2)

Model 10: Relationship between Wedge-tailed Shearwater Annexation and nest site characteristics

Annexation ~ Nest Type + Location + Burrow Length + Burrow Curve + Burrow Entrance Size, family = binomial (link = logit)

'Annexation' = nest site annexed or not annexed by a Wedge-tailed Shearwater

'Nest Type' = earthen burrow, vegetated nest scrape, or rock crevice

'Location' = study area 1, 2, 3, 4, 5, or 6

'Burrow Length' = burrow length (cm)

'Burrow Curve' = burrow curved or was straight

'Burrow Entrance Size' = burrow entrance size (cm^2)

CHAPTER 3

Model 1: Relationship between presence of *Monomorium pharaonis* and vegetation type (repeated for *Tetramorium bicarinatum, Monomorium floricola, Cardiocondyla nuda* and *Plagiolepis alluaudi*)

Presence ~ Vegetation Type, family = binomial (link = logit)

'Presence' = species present or absent from area

'Vegetation Type' = Categorized vegetation type (1, 2, 3, 4, or 5)

CHAPTER 4

Model 1: Relationship between ant population levels and treatment area

Ants ~ Treatment, family = poisson (link = log)

'Ants' = the number of ants collected in pitfall traps

'Treatment' = control or ant bait application

Model 2: Relationship between ant interactions and Tristram's Storm-petrel nest type

Interaction ~ Nest Type, family = binomial (link = logit)

'Interaction' = interaction between ants and chick recorded at nest (yes, no)
'Nest Type' = earthen burrow, vegetated nest scrape, or rock crevice

Model 3: Relationship between ant visitation and Bonin Petrel burrow characteristics

Visitation ~ Burrow Diameter + Occupation + Location + Burrow Diameter * Occupation + Burrow Diameter * Location + Occupation * Location, family = binomial (link = logit)

'Visitation' = presence or absence of ants in burrow (yes, no)
'Burrow Entrance' = height * width of burrow entrance (cm^2)
'Occupation' = burrow occupied by a Bonin Petrel (yes, no)
'Location' = plot 1A, plot 1B, plot 2A, plot 2B

Model 4: Relationship between ant visitation and the presence of a Bonin Petrel chick

Visitation ~ Occupation + Burrow Diameter + Location + Occupation * Burrow Diameter + Occupation * Location + Burrow Diameter * Location, family = binomial (link = logit)

'Visitation' = presence or absence of ants in burrow (yes, no)
'Occupation' = unoccupied burrow, Bonin Petrel adult, Bonin Petrel chick
'Burrow Entrance' = height * width of burrow entrance (cm^2)
'Location' = plot 1A, plot 1B, plot 2A, plot 2B

Model 5: Relationship between the number of foraging ants and Bonin Petrel burrow characteristics

Ants ~ Burrow Diameter + Occupation + Location + Burrow Diameter * Occupation + Burrow Diameter * Location + Occupation * Location, family = poisson (link = log)

'Ants' = number of foraging ants
'Burrow Entrance' = height * width of burrow entrance (cm^2)
'Occupation' = burrow occupied by a Bonin Petrel (yes, no) 'Location' = plot 1A, plot 1B, plot 2A, plot 2B

Model 6: Relationship between the number of foraging ants and the presence of a Bonin Petrel chick

Ants ~ Occupation + Burrow Diameter + Location + Occupation * Burrow Diameter + Occupation * Location + Burrow Diameter * Location, family = poisson (link = log)

'Ants' = number of foraging ants
'Occupation' = unoccupied burrow, Bonin Petrel adult, Bonin Petrel chick
'Burrow Entrance' = height * width of burrow entrance (cm^2)
'Location' = plot 1A, plot 1B, plot 2A, plot 2B

CHAPTER 5

Model 1: Relationship between ant population levels and treatment area

Ants ~ Treatment, family = poisson (link = log)

'Ants' = the number of ants collected in pitfall traps

'Treatment' = control or ant bait application

Model 2: Relationship between avian tick population levels and treatment area

Ticks ~ Treatment, family = poisson (link = log)

'Ticks' = the number of ticks collected in pitfall traps

'Treatment' = control or ant bait application

Model 3: Relationship between fledge success and lay date

Success ~ Lay Date, family = binomial (link = logit)

'Success' = fledged chick or failed chick

'Lay Date' = week into the breeding season

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